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QUATERNARY ENVIRONMENTS AT CAPE DECEIT (SEWARD PENINSULA, ALASKA): A CONTRIBUTION TOWARDS AN UNDERSTANDING OF THE EVOLUTION OF TUNDRA ECOSYSTEMS

by

J. V. MATTHEWS, Jr.

A THESIS

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FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "Quaternary Environments at Cape Deceit (Seward Peninsula, Alaska): a Contribution Towards an Understanding of the Evolution of Tundra Ecosystems", submitted by J. V. Matthews, Jr., B.Sc., M.Sc. in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

ABSTRACT

Unconsolidated sediments at Cape Deceit near Deering, Alaska range in age from latest early Pleistocene to Holocene. Plant and insect fossils from these sediments, as well as certain sedimentary features, provide evidence for documenting evolution of the terrestrial ecosystem at Deering.

A tundra ecosystem functioned at Deering for most of the time represented by the Cape Deceit sedimentary sequence. The regional tundra environment of northern Seward Peninsula during early Pleistocene time was similar to that of the present; however, the local environment at Cape Deceit was quite different, being only scantily vegetated. Starting in the middle Pleistocene the regional tundra vegetation evidently became more grassy, a trend which culminated in steppe-tundra conditions during latest Wisconsin time.

Former periods of warmer climate at Deering are indicated by evidence for westward movement of treeline. The last time forest or forest-tundra existed at Deering was no later than the penultimate interglacial. Spruce treeline stood closer to but not at Deering during the Sangamon interglacial. At least once, during latest early Pleistocene time, treeline at Deering was comprised of larch instead of spruce.

Most ecosystem evolution which has occurred at Deering is of the non-phyletic type, i.e. involving little or no in situ evolution of plants and animals. The only definite evidence of evolution among insects during the 400,000 or more years represented by the Cape Deceit sequence is reduction of flight wings in Tachinus apterus (Coleoptera: Staphylinidae).

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INTRODUCTION

Recent papers by D.M. Hopkins (1967a; IN PRESS, 1972) have admirably summarized and collimated present knowledge of Quaternary geology, paleontology, and biogeography of the Beringian region, including eastern Siberia, western Alaska, and the intervening Bering and Chukchi epicontinental seas. Several gaps in our knowledge of the history of this area are also revealed by Hopkins' papers. The most glaring of these is the paucity of information on early and middle Pleistocene terrestrial environments in western Alaska--a result of the fact that sediments of that age in the area are predominantly near-shore marine in origin (Hopkins, 1967b). In contrast late Pleistocene environmental history of western Alaska is much better known (Colinvaux, 1967; Hopkins, IN PRESS, 1972); although much more work will be necessary to obtain paleoenvironmental data comparable to that now available in areas such as north central United States and western Europe. Much of this information will no doubt come from continuing palynological research in Alaska, but the most valuable studies are likely to be those employing a combination of several analytical techniques. Such a multifacetted study is the subject of this paper. Fossils of pollen, plant macrofragments, and insects from Quaternary sediments at Cape Deceit (Fig. 1; Guthrie and Matthews, 1971) are analyzed, and attention is also given to the possible paleoclimatic implications of certain sedimentary structures occurring at the exposure.

Oldest sediments at the Cape Deceit exposure are of latest early Pleistocene age (Cromerian); consequently, their fossils should help to alleviate the limited fund of knowledge on early and middle Pleistocene terrestrial environments. Some of the results are unexpected.

For example, sediments from the lower part of the exposure document several climatic fluctuations during which conifers expanded their western limit to include Deering and Cape Deceit. One such fluctuation saw existence of a larch treeline in the Deering region. Also of significance is the fact that the oldest sedimentary unit at Cape Deceit contains the first North American record of the Eurasian rodent genus, Pliomys (Guthrie and Matthews, 1971) and the most primitive representatives of small mammal lineages whose contemporary members dominate tundra faunas.

Dating of the upper portions of the Cape Deceit sequence is open to question; however, it certainly includes sediments of late Wisconsin age. The fossils from them also offer some surprises in the form of grassland insects which are either very rare or do not occur at all in Alaska today as well as other insects which imply significant differences in substrate pH and other environmental parameters. In other words, pollen, plant macrofossil and insect fossil data discussed below show clearly that the present tundra environment is quite different from that which existed in Alaska as late as 12,000 years ago. In as much as such differences are revealed by changes through time of both the biotic and abiotic environment (due ultimately to climatic change), the paleoenvironmental record presented here is actually a history of ecosystem change--ecosystem evolution.

METHODS

I. POLLEN SAMPLES

Pollen samples discussed here have been prepared using a modified version of a schedule developed by Mehringer (1967) specifically for alluvial pollen samples. My modifications (greater number of swirls, prolonged HF treatment, and elimination of HNO_3 treatment) help to concentrate sufficient pollen for analysis, often a problem with samples representing tundra, while at the same time insuring preservation of the partially degraded pollen usually occurring in colluvial sediments.

II. MACROFOSSILS

The initial step in Mehringer's procedure of processing pollen is to wash approximately 50 ml of sediment through 0.254 mm screen in order to remove large organic and mineral fragments. Residue left on the screen often contains plant and insect macrofossils, providing, in some cases, alternate evidence for interpretation of pollen data.

Large sediment samples (200 + kg) from selected levels in the Cape Deceit exposure were processed in order to obtain large assemblages (samples) of plant and insect macrofossils. Silts and peaty silts were first sieved with 0.635 mm screens at the fossil locality. The residue was then sieved again with 0.317 mm screens in the laboratory to remove remaining silt and clay. Next, seeds were skimmed from the floating fraction of the residue, and if extremely abundant, a randomly selected sub-sample was used for analysis (see PLANT MACROFOSSILS). Finally the insect fraction of the original sieve residue was concentrated using a flotation technique developed by Coope (1961). A dissecting microscope was then used to isolate identifiable insect

fragments which were either stored in alcohol or immediately glued to macrofossil slides.

Samples of felted (bedded) peat, which occur at some levels in the exposure, were processed differently since they often contain exceptionally well preserved, partly articulated insect fossils. Such peat samples were collected in blocks and carefully pried apart in the laboratory. Articulated fossils were removed individually and glued to macrofossil slides. Partially articulated insect fossils occasionally occurred also in carbonate cemented silt peds.

III. IDENTIFICATION AIDS

Pollen and spores were identified using keys, illustrations in current palynological literature (Faegri and Iversen, 1964; Erdtman, 1965, 1966, 1969; Erdtman *et al.*, 1961, 1963; Beug, 1961) and reference slides. Herbarium specimens, as well as keys and illustrations in Berggren (1969), Beijerinck (1947), Bertsch (1941), Brouwer and Stahlin (1955), Martin and Barkley (1961), and Katz *et al.* (1965), aided identification of plant macrofossils. Insect fossils were identified mainly by the author using comparative material in his own and museum collections. K.G.A. Hamilton identified Homoptera fossils; W.R.M. Mason examined some of the Hymenoptera fossils; M.J. Campbell checked *Tachinus* and *Micralymma* determinations; C.H. Lindroth examined specimens of *Harpalus* cf *alaskensis* Lth.; and R.E. Leech identified spider fossils.

The entire fossil collection is presently in the author's possession at the Geological Survey of Canada (Ottawa). A permanent repository will be chosen at a later time.

GEOGRAPHIC AND BIOTIC SETTING

Quaternary exposures discussed here occur adjacent to Cape Deceit, a prominent landmark in the low-lying northern coastal region of Seward Peninsula (Figs. 1, 2). Deering, a small Eskimo village at the mouth of the Inmachuk River, is within four kilometers of the Cape and Quaternary exposures (Fig. 1). Deering is in a region of continuous permafrost. Mean annual temperatures range from -4 to -8°C, and mean annual precipitation is between 130 and 150 mm (Hultén, 1968).

Local bedrock in the Deering region consists mainly of Paleozoic metalimestone (exposed at Cape Deceit) and schistose pelitic rocks of Paleozoic age, locally covered by Cenozoic basalts to the south and west of Deering (Hopkins, 1963; Hopkins et al., 1971). Surficial sediments in the area are mostly primary and reworked loess that is capped in most areas with a thick sedge or moss turf. Coarse alluvium is in the valleys of the larger rivers such as the Inmachuk (Fig. 2). Marine sands and gravels, as well as estuarine detrital peats, are in areas which were inundated or formed shorelines during the last, or Sangamon (=Pelukian) interglacial.

Northern coastal portions of the Seward Peninsula have never been glaciated. During Illinoian time glaciers existed in the headwater region of the Kiwalik River, southeast of Deering (Fig. 2). To the north Illinoian glaciers originating in the western Brooks Range approached as close to Deering as Baldwin Peninsula (Fig. 2). Outwash streams emanating from that area and flowing across the then dry floor of inner Kotzebue Sound (Fig. 2) would have provided an ample source for loess deposited in the Deering area. Different conditions prevailed during Wisconsin time. Glacier termini were more distant from

the Deering region, and outwash streams originating in the western Brooks Range were prevented from a close approach to Deering by the terminal moraine complex now forming part of Baldwin Peninsula. Thus the amount of loess deposited at Deering during Wisconsin time was much less than during the Illinoian.

Deering and Cape Deceit are presently within a region of shrub tundra (Zone 4 of Young, 1971; "hypoarctic tundra" of Yurtsev, 1972). A detailed discussion of the flora and vegetation of the Deering-Cape Deceit area is not within the scope of this paper; however, a few general comments are required. Silty soils of the uplands near Deering support an Eriophorum tussock-dominated tundra in which certain heaths (Ericales) and prostrate shrub birches (Betual nana) are also common. Dryas fellfield frequently occurs in dry areas with poorly developed soils. Sedges and mosses dominate moist areas of the lowlands; but where soil is especially peaty, Rubus chamaemorus (Salmonberry), Empetrum nigrum (Crowberry), and dwarf birches are abundant ("Cloudberry dwarf shrub marsh" Hanson, 1953). On sunny slopes and floodplains of the larger rivers grow alders, shrub willows, and dwarf birches taller than the prostrate forms existing elsewhere.

Shrub willows also occur near inactive peat rings and at the margins of now stable solifluction lobes on the uplands. Throughout the Deering region, grasses are relatively rare, except at very dry sites. Artemisia was observed growing only on the unstable, deeply thawed coastal bluffs.

Detailed descriptions of the vegetation in other areas of western Alaska are outlined in Hopkins and Sigafoos (1950), Hanson (1953), and Johnson et al. (1966). The latter report, dealing with the Cape Thompson area, describes several "vegetation types" which also occur

in the Deering region. Papers concerned with more northern parts of Alaska (Hultén, 1968; Wiggens and Thomas, 1962; Britton, 1966) show that some important plants of the Deering region--e.g. Betula, Alnus--do not occur farther north (Young, 1971). A more severe regional climate is probably the cause.

Spruce treeline is located approximately 75 km east of Deering (Fig. 2), although isolated outliers of spruce occur within 40 km of the town. Figure 2 shows that spruce treeline in the Kotzebue Sound area possesses a marked eastern re-entrant which is not duplicated in other coastal areas of Seward Peninsula (e.g., on the south side of the peninsula, Fig. 2). This may be an effect of relatively cold surface waters in Kotzebue Sound (Fleming and Heggarty, 1966).

The insect fauna of western Alaska is poorly documented. Even faunal lists from such intensively studied sites as Cape Thompson (Fig. 1) (Watson, et al., 1966) contain obvious omissions. Nevertheless, the scanty knowledge which is available indicates that shrub tundra sites such as Deering are inhabited by an insect fauna with strong Hudsonian affinities (W.R.M. Mason, Pers. Comm., 1971), implying that the tundra fauna there is not radically different from that in forested areas immediately to the east. Greatest forest versus tundra faunal distinctions probably exist among the Coleoptera (beetles), since several obligate tundra beetle species occur at Deering.

STRATIGRAPHY AND CHRONOLOGY

I. STRATIGRAPHY

Stratigraphy of the Cape Deceit exposures has been discussed in detail by Guthrie and Matthews (1971) and is presented diagrammatically in Figures 3, 4, and 5. Three major stratigraphic units--Cape Deceit Formation, Inmachuk Formation, Deering Formation--are recognized. These have been subdivided into a number of minor stratigraphic units, such as Peat 1, Unit 1, etc. Mutual contacts of the three formations are angularly unconformable and otherwise characterized by distinctions of sediment, color, and texture (Guthrie and Matthews, 1971). Organic silt is the dominant sediment in all three formations; however, some units contain lenses of sand or gravel as well as laterally continuous peat horizons (Figs. 3, 4).

Correlation of some of the peat horizons here differs from that given in Guthrie and Matthews (1971). In that report Peat 6 at Station 1 was described as consisting of two peat horizons separated by a thin band of silts (sample 47-69, Fig. 7). I now feel that the designation "Peat 6" should be restricted to the lower peat (source of C^{14} sample I-4780, Fig. 5). The thick upper peat at Station 1 is probably equivalent in age to the late Holocene blocky, moss peat occurring at other parts of the Cape Deceit exposure (e.g., site of sample 72-67, Figs, 7, 10) as well as at other sites in the Kotzebue Sound region.

Figure 6E shows Peat 5 and associated sediments at one part of the exposure at Station 8 (Fig. 4). Toward Cape Deceit Peat 5 merges with overlying organic silts and peaty silts (samples 99-68 and 100-68) to form a single organic horizon. Accordingly, the designation "Peat 5" at Station 8 applies to the actual peat horizon as well as immediately

overlying organic silts. Thus, samples 99-68, 100-68, and probably even macrofossil assemblage (sample) S-5 (Fig. 7) should be considered to be within the Peat 5 stratigraphic unit. Pollen evidence presented below shows that organic sediments of basal Unit 2 at Station 1 should not be referred to Peat 5 as is done in Guthrie and Matthews (1971).

II. CHRONOLOGY

Arguments on the probable age of the Cape Deceit Formation and overlying sediments have been stated elsewhere (Guthrie and Matthews, 1971). A detailed, slightly revised compilation is given in Figure 5. Paleoenvironmental data presented in this paper and other information not available before 1971 make necessary further discussion of the Cape Deceit chronology. Important dating criteria used in that discussion are: (1) radiometric dates (Deering Fm. only); (2) stage of evolution of certain mammalian taxa; (3) fossil evidence of a more western position for treeline; and (4) sedimentary features indicative of thawing and erosion.

Cape Deceit Formation

Mammalian fossils from the Cape Deceit Local Fauna, hereafter referred to as the CD Local Fauna, provide the best evidence for dating the Cape Deceit Formation. Comparable mammalian assemblages exist only in the Palaearctic, hence the use of European terminology in Figure 5. Local Alaskan correlation is difficult since the early and middle Pleistocene of the State is represented primarily by near-shore marine sediments (Hopkins, 1967b)--not the type to contain vertebrates such as those from Cape Deceit.

In the previous report on Cape Deceit (Guthrie and Matthews, 1971) the stage of evolution of three newly described small mammal taxa

from the CD Local Fauna--Microtus deceitensis, Pliomys deeringensis, Predicrostonyx hopkinsi--was taken to mean that the Cape Deceit Formation is of pre-Cromerian age. As long as the term "Cromerian" is applied to a single pre-Mindel interglacial, this conclusion is still valid and is substantiated by recent evidence from Siberia. But in the discussion below "Cromerian" is used in a more extensive sense (Zagwijn, et al., 1971), making the entire Cape Deceit Formation Cromerian rather than pre-Cromerian in age.

Evidence from eastern Siberia for the age of the Cape Deceit Formation is based on fossil mammals of the Olyor Suite on the Chukochya River (Kolymian Lowland) (Sher, 1971). Olyor small mammals include a species of Microtus equally as primitive as M. deceitensis and a species of Dicrostonyx which is slightly more advanced dentally than Predicrostonyx hopkinsi (A.V. Sher and V.S. Zazhigin, Pers. Comm., 1970). The Equus terminal phalanx illustrated in Guthrie and Matthews (1971) is thought by Sher (Pers. Comm., 1970) to represent the Olyor species E. (Plesippus) verae, while the illustrated Equus premolar probably represents a species more advanced than the Villafranchian E. (Plesippus) stenonis. In Sher's and Zazhigin's opinion these facts suggest that the CD local fauna predates the oldest assemblage in the Olyor Suite. Olyor assemblages are considered to be the Siberian equivalent of the middle European Mindel-Mindel/Riss Tiraspol fauna (Gromov, 1970; Vangengeim and Sher, 1970), which means that the CD Local Fauna and the Cape Deceit Formation are older than Mindel (=Elster). Furthermore, since the Cape Deceit Formation occurs below an unconformity that resulted from interglacial thawing and erosion, the formation probably predates not only the European Mindel (Elster) but also the interglacial immediately preceding it.

I have referred to this interglacial as the Cromerian (Guthrie and Matthews, 1971), but the Cromerian stage is actually a complex of several glacials and interglacials (Zagwijn, et al., 1971; West and Wilson, 1966); so if that term is to be used at all with reference to the Cape Deceit Formation, it should be applied to the entire formation, which also includes several glacial and interglacial fluctuations (Fig. 5). The term "Cromerian" is used here in the same way as in The Netherlands where it denotes the series of glacial-interglacial fluctuations predating the Elster glaciation and post-dating the early Pleistocene Menapian glaciation (Zagwijn, et al., 1971; Van der Hammen, et al., 1971). Radiometric and paleomagnetic dating show that in Europe it represents the time interval 400,000 to 900,000 years BP. Thus these dates reflect the probable minimum ages for deposition of the Cape Deceit Formation.

More precise correlation of the Cape Deceit Formation should be possible in the near future, since an attempt to date the sediments paleomagnetically (as in Zagwijn, et al., 1971) is being planned. Also, fossils of Pliomys and a very primitive species of Microtus have recently been discovered in Saskatchewan (A.M. Stalker, Pers. Comm., 1972). When these are studied and compared with Cape Deceit fossils, they should allow correlation of the Cape Deceit Local Fauna with one of the established North American Land Mammal ages. An attempt should also be made to date Cape Deceit bones using a technique recently outlined by Bada (1972). A prerequisite of the method is that the bones have had a stable temperature history. Though this cannot be assured for the Cape Deceit fossils, they have undoubtedly undergone less fluctuation of temperature than fossils from any terrestrial assemblage of comparable age.

Inmachuk Formation

A single Pliomys molar was found in the lower sands of the Inmachuk Formation. Because Pliomys does not occur in early or late Pleistocene faunas of eastern Siberia, yet must have passed through that area to get to North America (it is of Palaearctic derivation), this single fossil tends to indicate that the Inmachuk Formation is also of pre-Olyor (pre-Mindel) age. But if the single fossil was rebedded from the Cape Deceit Formation then all that can be said of the age of the Inmachuk Formation is that it predates Deering Formation Unit 1, shown in the following discussion to be of probable Illinoian age (Fig. 5).

Deering Formation

C^{14} dates show that Unit 2 of the Deering Formation is of Wisconsin and Holocene age. Peat 5 is older than 39,900 years (Fig. 5). Since it represents a warmer climate (see POLLEN ANALYSIS) and occurs below late Wisconsin sediments, it is likely to be either of Wisconsin interstadial or Sangamon interglacial age.

Presence of Dicrostonyx henseli Hinton fossils at the base of Unit 1 (henseli Zone) was previously cited (Guthrie and Matthews, 1971) as evidence that Unit 1 is of Illinoian age, which would imply in turn that underlying Peat 4 is of Kotzebuan interglacial age (=Kotzebuan marine transgression) and that Peat 5 is of Sangamon age.

The essence of the argument is that the extinct lemming D. henseli is assumed to be the immediate ancestor of the extant D. torquatus Pallas, meaning that Cape Deceit sediments containing D. henseli predate the earliest (late Illinoian) Alaskan record of D. torquatus, providing, of course, that D. henseli fossils do not represent a relict population. Relict populations of D. hudsonius (Pallas),

a species very similar to if not conspecific with D. henseli, occur today on the tundra east of Hudson Bay, but no such pronounced geographic barrier ever separated tundra environments in central and western Alaska; so D. henseli likely occurred in the latter area only before evolution of D. torquatus. Recently, however, an M_3 morphologically intermediate between those in D. henseli and D. torquatus was found in Wisconsin age sediments at Cape Espenberg (Fig. 2) (D.M. Hopkins and C.A. Repenning, Pers. Comm., 1971). But this fact does not necessarily invalidate the assumption that D. henseli fossils predate D. torquatus since such intermediates are to be expected in the evolutionary progression from one to the other; and moreover, they are sure to occur if, as some workers believe, D. henseli and D. torquatus are merely temporal variants to a single species.

Other facts also suggest that Unit 1 of the Deering Formation is of Illinoian age. These are:

(1) Primary loess thickness in the Deering Formation exceeds three meters (usually in Unit 1 alone); whereas, D.M. Hopkins (Pers. Comm., 1972) reports observing a loess cover only one meter thick on gravel making up a spit of Sangamon age on the west side of Kugruk Lagoon, 10 km east of Deering. If this observation is a valid index of thickness of Wisconsin age loess in the Deering area, then the Deering Formation must represent more than just Wisconsin and Holocene time. Almost all of the primary loess in the Deering Formation occurs in Unit 1--to be expected if it is of Illinoian age since outwash streams (probable source of the loess) at that time, would have passed quite near the present site of Deering and Cape Deceit (see GEOGRAPHIC AND BIOTIC SETTING and Fig. 2).

(2) Differences in the stratigraphy above Peat 4 at Stations

8 and 9 suggest that Pelukian gravels and Peat 4 are not synchronous. If they were, then a high degree of similarity would be expected in the stratigraphy of the two adjacent exposures. This is not the case. Instead, sediments overlying Peat 4 at Station 9 consist of a relatively thick sequence of organic, peaty silts and contain no evidence of Unit 1 loess or the "frost cracks" which are so evident at Station 8 and all other parts of the exposure nearer Cape Deceit. A probable explanation for this distinction is that Station 9 is very close to the former position of a Pelukian shoreline (note proximity of Pelukian beach gravels--Fig. 4) and its stratigraphy is of the type expected in an area of eroding unconsolidated coastal bluffs. Similar sequences of organic silts, containing buried mats of plants, are forming over erosion resistant Peat 1 along the present coast. Peat 4, like Peat 1, is fibrous and compact, qualities likely enhancing its preservation in exposures at both Stations 8 and 9.

If the above explanation is correct then Pelukian gravels at Station 9 and Peat 4 cannot be of the same age since Pelukian coastal erosion has removed a sequence of sediments (Unit 1) that at Station 8 overlie and postdate Peat 4. Thus Peat 4 predates Pelukian gravels and most likely represents the preceding Kotzebuan interglacial. Peat 5, dated at greater than 39,900 years, is therefore judged to be the Pelukian (Sangamon) equivalent (Fig. 5).

Though I believe the above evidence to be persuasive, it is certainly equivocal. Therefore, Figure 5 includes an alternate interpretation based on the assumption that Peat 4 and Pelukian sediments at Station 9 are correlative. Under this scheme Unit 1 of the Deering Formation would represent early Wisconsin time, and the Inmachuk Formation might be no older than the Illinoian. The presumed age of the Cape Deceit Formation would, however, remain unchanged.

PALEOENVIRONMENTAL DATA

I. SEDIMENTARY FEATURES

Certain sediments and sedimentary structures exposed at Cape Deceit have paleoenvironmental significance. The following discussion concerns such features as well as others of lesser or unknown significance.

Wedge-Shaped Features

Several types of wedge-shaped sedimentary structures occur in the Cape Deceit exposure. One of these, an ice wedge pseudomorph, has unequivocal paleoenvironmental implications, but other types, which might be mistaken for ice wedge pseudomorphs, are of different origin and of less certain paleoenvironmental significance.

a. Ice wedge pseudomorph:

An ice wedge pseudomorph occurs within the upper part of Unit 2 of the Cape Deceit Formation between Station 2 and 3 (Figs. 3, 6B). This single feature indicates that permafrost existed in the Deering region when the ice wedge formed (Péwé, 1966); however, it is not possible to tell from the form of the pseudomorph alone if the ice wedge developed during or after deposition of Unit 2 sediments. But other evidence, such as sharply bounded silt clasts in which original bedding is rotated with respect to bedding of host sediments, confirms presence of permafrost during Unit 2 time.

Following formation of the ice wedge, it melted and was replaced by a sediment pseudomorph. Thaw lake formation, a natural phenomenon in permafrost areas, can result in such melting; however, if this were the case for Unit 2, the sediments of the pseudomorph as well as those capping it would have a lacustrine character. They do not; hence, the pseudomorph as well as the erosion following Cape Deceit sedimentation

and slumping of Unit 2 sediments (note the steeply dipping Peat 2 near Station 5) probably all result from an interval of regional climatic warming (an interglacial). Since ice wedges are presently forming in the Deering area, climate would necessarily have been warmer than at present, and was perhaps more like that of comtemporary interior Alaska.

b. "Frost cracks":

An important marker horizon in the Deering Formation is a zone of small wedge-shaped features provisionally termed "frost cracks" in a previous report (Guthrie and Matthews, 1971). For purposes of continuity, I use that term here even though reassessment of the features suggests that they may be desiccation cracks instead.

Where best developed, the "frost crack" zone consists of narrow wedges, 30-40 cm apart, originating rather abruptly at particular level within Unit 1 (Deering Fm.) and penetrating to depth of 40-80 cm (Fig. 6A). Ferruginous bands bordering the wedges are sharply downturned at some levels and have a sharp contact with the gleyed wedge filling. Cracks taper to a narrow ferruginous-bordered seam in the lower part of Unit 1 where inorganic loess gives way abruptly to the more organic silts of the henseli zone (Figs. 4, 5 and Guthrie and Matthews, 1971). Thicknesses of the wedge fillings vary, but many are narrower at the top of the "frost crack" zone, indicating syngenetic development (Dylik, 1966; J. Dylik, Pers. Comm., 1969). In plan view the "frost cracks" form poorly defined circular to polygonal nets.

Empirical data, as well as theoretical calculations on the mechanics of ice wedge formation (Lachenbruch, 1962, 1966; Washburn, 1969), show that ice wedge polygons must be larger than one or two meters in

diameter. Thus the "frost cracks" representing polygons less than a meter in diameter cannot be ice wedge pseudomorphs, despite the close resemblance. If permafrost existed in the Deering region during formation of "frost cracks" (see pollen evidence presented below), they must have been restricted to the active zone.

Zones of small-scale wedge-shaped features occur in late Pleistocene exposures in Belgium (Paepe and Pissart, 1969; Paepe and Vanhorne, 1967) and Holocene sediments at the Onion Portage archaeological site in western Alaska (C.S. Schwegar, Pers. Comm., 1969). I have observed small non-sorted polygons bordered by vertical cracks in a Dryas-dominated area at Cape Deceit. Though superficially similar to "frost cracks" from Cape Deceit, all of these features differ by being associated with an underlying involution zone; hence, they probably do not have exactly the same origin as the Cape Deceit features. Washburn (1969) illustrates small-scale disiccation cracks from northeastern Greenland that more closely resemble the "frost cracks" of Unit 1. They are forming, as the "frost cracks" evidently did, in an environment of continuing silt deposition where vegetation is scanty (note the inorganic character of Unit 1 loess--see INVERTEBRATE FOSSILS). Humic materials accumulate in surface depressions associated with the vertical cracks in eastern Greenland (Washburn, 1969). If similar conditions existed during formation of "frost cracks", then the gleyed character of the wedge fillings would be explained (Siuta and Motawicka-Terelak, 1969). At many of the Cape Deceit exposures, the "frost crack" zone has an abrupt upper limit. An analagous situation occurs in eastern Greenland where development of the cracks has apparently been arrested by a pulse of rapid sediment deposition. Increased loess

deposition at Cape Deceit during Unit 1 time might have had a similar effect on the growth of "frost cracks" since it would preclude repeated cracking at the same locus--chief factor responsible for the well defined character of the "frost crack" zone. Figure 6A shows that a few small cracks do exist above the upper limit of the "frost crack" zone, but they are not as obvious since they do not coincide with the original syngenetic cracks.

Thus, the "frost crack" zone in Unit 1 of the Deering Formation evidently formed under a special combination of climatic and depositional conditions, explaining why similar "frost crack" zones are not present in other parts of the exposure. Since "frost cracks" are most similar to the east Greenland features described by Washburn (1969), they probably have a similar origin--desiccation cracking. Most importantly, they are not related to ice wedges and therefore, imply nothing about the presence or absence of permafrost.

c. Loess gullies:

Larger wedge-shaped structures, also superficially similar to ice wedge pseudomorphs, occur in the "frost crack" zone of Unit 1 (Fig. 6F). Host sediments are not slumped at the contact with the wedge, and sediments filling the wedge are horizontally bedded, thus ruling out the possibility that these structures are ice wedge pseudomorphs. Instead they are probably small loess-filled gullies such as those observed at exposures in Poland (Dylik, 1966). If so, they indicate little about the former environment except that loess deposition during Unit 1 time was intermittent.

Peat 5 sediments clearly signal cessation of Unit 1 loess deposition and possibly the onset of climatic change. A zone of discolored and leached silts immediately below Peat 5 at Station 8 represents

an incipient soil, formed during development of the nodular peat horizon (Fig. 6E). The lower boundary of the weathered zone is accentuated by a concentration of humates, possibly marking a former long-standing position of permafrost table; but if so, the thickness of the active zone during the first phase of Peat 5 formation would have been no more than 30 cm.

Solifluction

Solifluction, a special type of congeliturbation involving down-slope movement of soil and vegetation, has played a significant part in deposition of some sediments at the base of the Cape Deceit exposure (Guthrie and Matthews, 1971). Folded sediments, especially peats, at other parts of the exposure may be evidence of other periods of solifluction activity. For example, folds of Peat 2 near Station 2 (Fig. 3) are similar to those seen in cross sections of contemporary solifluction lobes containing buried surface organics (Hanson, 1950; Benedict, 1970). Some folds of Peat 2 are conformable with deformational structures in the upper part of the overlying Inmachuk Formation; therefore, most, if not all, of the congeliturbation of the peat and associated sediments occurred long after deposition of the Cape Deceit Formation (possibly even after deposition of the Inmachuk Formation) and before initial deposition of the Deering Formation.

Some puzzling structures are found in the upper part of the Inmachuk Formation. Truncated folds of peaty sediments (Peat 3--Fig. 6D) occur at the contact of the Inmachuk and Deering formations. These are analagous to non-truncated structures observed near the boundary between Unit 1 and Unit 2 at the Station 8 exposure of the Deering Formation (Fig. 4). In neither case is solifluction likely to be the

sole cause because both sets of features (especially some of those in the upper part of the Inmachuk Formation--Fig. 4, near Station 5) possess folds implying opposite sense of motion, an unlikely situation if they are due to solifluction alone. Symmetrical folds like those in the upper Inmachuk Formation might be due to growth of peat rings or similar non-sorted polygonal features (Hopkins and Sigafoos, 1950) except that the folds in such features often result from lateral thrusting of frost-churned sediments. Well preserved overturned frost or desiccation cracks seen in the Inmachuk folds would have been obliterated in such milieu. Thus, Inmachuk folds are probably not due to formation of unsorted polygons.

All that can be concluded is that some of the folds within the Cape Deceit exposure obviously result from solifluction, while others were created by some as yet undetermined form of congeliturbation. A cold climate and moist substrate, but not necessarily permafrost, is indicated.

"Kittik"

"Kittik" is an Eskimo term applied to the pale yellow, silt and sand-size calcareous weathering residuum exposed at the base of the exposure near Station 1 (Fig. 3) (Guthrie and Matthews, 1971). Close examination of "kittik" sediments reveals that they result from mechanical weathering of the metalimestone bedrock, and thus probably originated during a period of periglacial climate. The lateral extent of the "kittik" unit is unknown, but it probably dips below the present beach level well before Station 2 (Fig.3). If so, it is one of the oldest Quaternary units at Cape Deceit, predating even the lowest exposed levels of Cape Deceit Formation Unit 1 (Table 6).

II. POLLEN ANALYSIS

Pollen Diagrams

Compilations of pollen data are presented as pollen diagrams (Figs. 8, 9, and 10). Stratigraphic position of the samples referred to in the diagrams is given on the diagrams and in Figure 7, which is a simplified version of Figures 3 and 4.

Several departures from standard methods of presenting pollen data have been made. (1) Some stratigraphic units were sampled more than once at different parts of the exposure in order to test the lateral continuity of the pollen spectra and provide additional information on the former regional pollen rain. (2) Bar diagrams are used instead of the traditional interpolated histograms where: (a) samples were not part of a vertical sequence; (b) the vertical sample interval was too great to justify interpolation; and (c) differences between adjacent spectra are obviously related to the type of sediment sampled. (3) Local pollen zones have not been designated because grouping the pollen samples by stratigraphic units serves adequately in organizing the pollen data into units for easier interpretation. Pollen sequences within stratigraphic units are neither long enough nor are the variations consistent enough to warrant zonation.

In the pollen diagrams solid horizontal lines separate groups of samples derived from a single stratigraphic unit. Dashed lines are used where a sample series crosses a stratigraphic boundary. The terms "Indet. Pollen" (indeterminate pollen) and "Undet. Pollen" (undetermined pollen) are used to indicate respectively (1) pollen too degraded for identification and (2) pollen well enough preserved for identification, but not identified. Finally, vertical scales are used in the diagrams

only where they apply to vertical series of closely spaced samples. The relative vertical position of other samples is obtained from Figure 7.

Ecologic and Taxonomic Notes

a. Diporate Gramineae pollen:

Grass pollen is monoporate; however, certain polyploid grasses and cereal hybrids (e.g. Triticale = Triticum X Secale) have diporate, multiporate, or inapertuate pollen (Erdtman, 1969; Erdtman, et al., 1963). Pollen sample 56-69 (Deering Fm.) includes an abundance of diporate grass pollen, indicating that polyploid or hybrid grasses occurred at the site during its deposition.

b. Thalictrum:

Two species of Thalictrum occur in interior and western Alaska but only T. alpinum is found on the tundra (Hulten, 1968). Even though pollen of the two species cannot be distinguished, macrofossils of T. alpinum (Fig. 13E) imply that Thalictrum pollen from Cape Deceit Formation samples represent alpinum.

c. Moss spores:

The fact that Sphagnum alone is listed in the pollen diagrams, does not mean that other mosses are absent. Many moss spores undoubtedly go unnoticed or are not preserved.

Surface Samples

Figures 1, 2, and 10 and Table 1 include information on five surface pollen samples from the Deering region. Together with other samples from the Imuruk region (Colinvaux, 1964; Colbaugh, 1968) they provide some insight for interpretation of the Cape Deceit fossil pollen spectra.

First, Deering and Imuruk surface samples give a general indication of the regional pollen rain in shrub tundra areas of Seward peninsula. The pollen rain of such areas is characterized by relatively high percentages of Betula, Alnus, and sedge (sometimes grass) and low percentages of Picea and Artemisia.

Second, the Deering surface samples in particular show most clearly the degree to which components of local plant communities may dominate pollen spectra (i.e.,"local over-representation"). Note, for example, the high percentage of Ericales pollen in sample 105-69 and its occurrence in an area where the ericads Empetrum nigrum and Vaccinium uliginosum are abundant (Table 1). Many of the fossil samples discussed below are from sediments similar to those used for surface samples, and therefore might also be expected to show similar degrees of local over-representation.

Third, certain of the surface samples illustrate a source of error--differential pollen production at the intra-specific level--which is not often mentioned in discussions of error in pollen analysis. Spruce pollen is relatively abundant in surface sample 97-69, despite the fact that it must all be allochthonous (Table 1). No doubt its abundance is related to the fact that spruces in present day western Alaska are expanding their range (Hopkins, IN PRESS, 1972). Under such conditions sexual reproduction, involving abundant pollen production, is dominant; but would this also be the situation were spruce treeline, located as at present, receding as a result of cooling climate? Recent studies on the effect of cold on conifer reproduction (Eiche, 1966; Eriksson, 1968; Dogra, 1967; Andersson, 1947) indicate a negative answer for this question. Cold stress causes meiotic disturbances of the

pollen mother cell and an increased incidence of apomixus and self pollination, which tend to either reduce production or its dispersal. It is possible to envision a condition in which the few surviving apomictic spruce of an area produce so little pollen that they go unrepresented in pollen spectra. A similar condition, involving a different plant, may be illustrated by the very low percent of Rubus chamaemorus pollen in surface sample 97-69 (Fig. 10), derived from an area where this species is dominant (Table 1). Apomixus is common in northern populations of R. chamaemorus (Salisbury, 1942).

Interpretational Criteria

The most fundamental level of paleoenvironmental resolution one could hope to obtain from the Cape Deceit pollen samples is ability to distinguish samples representing forest from those representing tundra. For this, Picea percentages are critical because at present (as well as during most of the Pleistocene) spruces occur at regional and altitudinal treeline. Unfortunately, the vagility of spruce pollen makes it difficult to derive a foolproof rule that would indicate the percentage of spruce pollen indicative of spruce forest. In most cases, however, Alaskan samples with at least 15 percent spruce and comparable amounts (or more) of Betula and Alnus indicate presence of spruce trees in the local environment (Rampton, 1971; Matthews, 1970). Very low percentages of Picea, when not due to over-representation of another pollen type, usually indicate tundra conditions.

A secondary level of resolution to be hoped for is recognition of different types of former tundra environments. In previous Alaskan studies (Colinvaux, 1967; Colbaugh, 1968) pollen evidence alone has been used to distinguish between shrub tundra that is dominated by dwarf birches with some alders; shrub tundra that possesses dwarf birches, but no

alders; and herbaceous tundra that lacks dwarf birches and alders. Such distinctions are most validly drawn when based on lacustrine rather than colluvial pollen samples because the former are more apt to represent past regional pollen rain--hence, past regional vegetation. However, in most colluvial pollen samples, high percentages of an anemophilous pollen type, such as that of Betula and Alnus, can be assumed to indicate former presence of the plant in the region, if not at the sample site itself. Low percentages, barring statistical bias, most often indicate that the plant was regionally rare. Ample reason for the qualifying words "most often" in this last statement is provided by surface sample 105-69 (Table 1). Though the sample site was within 30 mm of the nearest Alnus crispa bush, the alder pollen percentage is lower than in Imuruk Lake surface samples taken more than 10 km from the nearest alders (Colinvaux, 1964).

Pollen Data--Interpretation

a. Cape Deceit Formation (Unit 1):

Pollen sample 79-68 from the base of Unit 1 differs from all others in the diagrams by its combination of high percentages of Picea, Alnus and Botrychium and low percentages of sedge and grass pollen. It obviously represents a time when spruce trees grew very near or at the Cape Deceit locality.

Larches may also have grown near Deering during deposition of sample 79-68. Its content of Larix pollen is low, but possibly significant since even pure larch stands (at Edmonton, Alberta) yield surface samples containing as little as 10 percent Larix pollen (Matthews, unpublished data).

Without knowing the species of Botrychiun represented by spores from sample 79-68, it is difficult to attach any significance to the

high Botrychium percentage in that sample; however, in view of the low percentage of grass pollen, it is unlikely that the former environment was of the type in which B. lunaria (L.) and B. boreale (E. Fries), two western Alaskan species, now occur (Hultén, 1968).

Remaining Unit 1 spectra are more or less influenced by overrepresentation of sedge pollen; nevertheless, all clearly imply tundra conditions.

b. Cape Deceit Formation (Peat 1):

Sample 101-69 contains almost 10 percent Larix pollen, indicating that larches were definitely present locally when Peat 1 formed. Other evidence (see INVERTEBRATE FOSSILS and PLANT MACROFOSSILS) shows that the Deering area was near treeline at that time, but low Picea percentages suggest it was not a spruce treeline as is the case today. Instead larches must have marked the regional limit of trees, an unusual situation for North America--especially Alaska where Larix laricina is now recorded only from sites well within the regional limit of spruce (Hulten, 1968). In contrast larch treeline, formed of Larix dahurica Turce., does occur in present day eastern and northern Siberia (Komarov, 1934; Yurtsev, 1972)

c. Cape Deceit Formation (Unit 2):

Pollen spectra from this unit display a high degree of lateral and vertical consistency. They differ from those in other units by the following combination of characteristics: (1) low percentages of Picea and Alnus, (2) lower percentages of Betula than in most Seward Peninsula surface samples, (3) high percentages of sedge--exceeding grass percentages in most cases, (4) less than 15 percent Artemisia in all samples, but more than in surface samples, and (5) more than 5 percent Potentilla-Fragaria in most samples.

During Unit 2 time the Deering region must have possessed a tundra environment, but one differing from that of the present chiefly by extreme rarity of alders and lower abundance of dwarf birches. Regional climate was probably colder than at present; and, judging from the lower percentage of alder pollen, somewhat colder than during Unit 1 time.

Consistently high percentages of Potentilla-Fragaria pollen in Unit 2 samples undoubtedly reflect a long-standing feature of the local environment--most likely continuing silt deposition, which would promote the existence of semi-permanent pioneer seres similar to those in which many species of Potentilla occur today (see PLANT MACROFOSSILS). Potentilla palustris, a bog plant, is probably not the species represented by Potentilla pollen (see PLANT MACROFOSSILS).

d. Inmachuk Formation:

Most of the pollen data for this unit come from a series of samples taken at an exposure between Stations 2 and 3 (Figs. 7 and 8). The sample series does not extend to the upper portion of the formation because sediments there are folded, making determination of the vertical position of samples impossible.

Low percentages of Picea indicate tundra conditions. Samples from the base of the Inmachuk Formation are most similar to those from uppermost Unit 2 of the Cape Deceit Formation, but those higher in the Inmachuk sequence differ due to an increase in percentages of Betula and Sphagnum and a corresponding decline of Salix and Artemisia percentages.

Such a change of pollen frequencies might be ascribed to climatic change if not for the fact that it is correlated with

textural changes in the sampled sediments (Fig. 8), ranging from sands at the base to silts at the top of the sampled sequence. Accordingly, pollen frequency shifts more likely reflect a changing sedimentary environment rather than climatic change. An analogous sequence, though of a spatical rather than temporal character, has been documented in studies of arctic floodplain plant succession by Bliss and Cantlon (1957) and Viereck (1966). These studies show that feltleaf willows and herbs such as Artemisia dominate young floodplain areas where substrate consists of sands and gravels; whereas, those older parts of the floodplain where a silt substrate predominates possess a successional sere characterized by greater abundance of dwarf or shrub birches and mosses such as Sphagnum. High percentages of Salix in sandy sediments at the base of Unit 1 in the Cape Deceit Formation may also reflect substrate rather than climatic conditions.

Because sediments in the lower Inmachuk and upper Cape Deceit Formations differ texturally (Fig. 8), similarity of their pollen spectra may be largely fortuitous, with little or not regional environmental significance. Upper Inmachuk samples (from silts) provide a more valid basis for comparison with upper Cape Deceit Formation samples. They show that dwarf birches were probably more abundant during Inmachuk time, possibly due to milder climatic conditions. In contrast to Cape Deceit spectra, those from the upper Inmachuk Formation contain almost no Potentilla-Fragaria pollen, but the significance of this fact is difficult to determine since the plant macrofossil assemblage from the Inmachuk Formation (S-12, Fig. 7) is dominated by Potentilla achenes (Fig. 12).

e. Inmachuk Formation (Peat 3):

Salix pollen is over-represented in most Peat 3 samples. Solifluction and congeliturbation movements which occurred during and after deposition of Peat 3 may be the cause, in as much as such disturbances now create microhabitats favorable for willows, though not necessarily the same species which occur in early floodplain successional seres.

f. Deering Formation (Peat 4):

Taken together the three pollen spectra from Peat 4 (Figs. 9, 10) show that spruces, birches and alders were present in the Deering region. Extremely high percentages of Betula in two samples probably result from Betula resinifera, samaras of which occur in Peat 4 (see PLANT MACROFOSSILS).

A few pollen samples from organic silts immediately below Peat 4 indicate that a tundra environment, depauperate in alders, preceded the westward advance of spruces. In contrast, other studies from western Alaska (Colinvaux, 1964; Colbaugh, 1968) show that the westward expansion of spruces during the Holocene was preceded by tundra with abundant alders. Quite probably the sample interval below Peat 4 is too large to allow documentation of such a rise of alder percentages.

g. Deering Formation (Unit 1):

Guthrie and Matthews (1971) considered the thin peaty horizon of pollen sample 57-69 to be part of an interglacial complex including Peat 4. But the 57-69 pollen spectrum differs from those in Peat 4 by possession of a low Picea percentage. Thus, during deposition of 57-69 spruces were rare at Deering; however, they may not have been absent since a Picea macrofossil occurs in the pollen sample residue (Fig. 12). A situation, postulated earlier, in which apomictic spruces producing

little or no pollen continued to survive at Cape Deceit while climate cooled, would explain such apparently contradictory macrofossil and pollen evidence. Congeliturbation structures in sands underlying the thin peat from which 57-69 comes (Fig. 6) may represent the initial phase of climatic deterioration following Peat 4 formation. Deteriorating climate might also account for presence of polyploid grasses during deposition of the sands (sample 56-69, Fig. 6) (Johnson and Packer, 1967).

The henseli zone at the base of Unit 1 is poorly documented palynologically, but the few samples available do imply former tundra conditions. Most of the pollen spectra (with sample 58-69 being the glaring exception) contain less alder pollen than is common of contempory surface samples from Seward Peninsula.

Pollen documentation of the overlying inorganic "frost crack" silts is more complete. In addition to a series of samples from Station 8, samples from the top and bottom of the unit at other exposures are presented (Figs. 9 and 10). Low Picea percentages in samples of the series 59-69 to 68-69 (Fig. 9) show that Deering was within a tundra region and this is confirmed by scant macrofossil evidence (see INVERTEBRATE FOSSILS).

An interesting feature of the pollen sequence from Unit 1 is a trend toward high alder percentages at the top. It corresponds with no obvious sediment textural change, so is not likely (as in the case of the Inmachuk sample series) to be due to local substrate conditions. Pollen rain in fell-field areas, such as the one which evidently existed at Cape Deceit during deposition of the "frost cracked" silts, is often characterized by high percentages of allochthonous pollen.

But this cannot explain high alder percentages in Unit 1 because they occur also in basal Unit 2 sediments, which were not deposited under fell-field conditions (see INVERTEBRATE FOSSILS). Thus higher alder percentages in uppermost Unit 1 most likely reflect increase in regional abundance of alders, due perhaps to warming climate.

h. Deering Formation (Peat 5 and lower Unit 2, Station 8):

In Figure 9 the term "Peat 5" refers to the fibrous peat horizone seen in Figure 6E; however, as indicated earlier the peat is part of a sedimentary unit including immediately overlying organic and peaty silts. The sample from the peat (102-68) is biased by over-representation of grass pollen. Spectra from the associated organic sediments are characterized by higher percentages of alder pollen than in surface samples from Deering, implying a warmer climate and existence of alders in interfluve areas where they are rare today. Low spruce percentages in these samples indicate that climate was not warm enough to allow growth of spruces at Deering; however, in view of the constraints imposed by over-representation of alder pollen, spruce percentages in the lower Unit 2 sediments are probably actually higher than in overlying and underlying units. In other words, even though spruces did not occur at Deering, they no doubt were closer than at present.

i. Deering Formation (Unit 2):

Either lowermost Unit 2 sediments at Station 1 do not represent the same time interval as sediments in a comparable position at Station 8 or their pollen distinctions are evidence of extreme lateral variability in similarly aged pollen spectra. I favor the first alternative. Unit 2, if it represents the Wisconsin as indicated (Fig. 5) must possess numerous minor unconformities; therefore, unless supporting C^{14} data is

available, sediments in a similar position at different parts of the exposure can be considered correlative only in the broadest sense.

The same statement applies to correlation of platy silts in the upper parts of Unit 2 at Stations 1 and 8; although in this case synchronous deposition of at least the upper parts of the clayey silt zone are implied by the distinctive sedimentary character of the sediments and C^{14} dates. Pollen samples from clayey, platy silts at Station 1 and 8 are similar in their low content of spruce and alder pollen and high percentage of grass and Artemisia. A cold treeless environment is certainly indicated, but in view of grass and Artemisia percentages it should be referred to as a steppe-tundra rather than tundra, for the latter implies conditions like those of present tundra, whereas the fossil pollen spectra resemble no known surface samples from contemporary tundra sites in Alaska.

I have suggested that caution must be used in assuming that high grass percentages in pollen spectra necessarily represent grassland conditions or that Artemisia peaks indicate anything more than local abundance of Artemisia (Matthews, 1970; and unpublished manuscript). But in this case, plant macorfossils and insect fossils strongly confirm pollen evidence of cold grassland or steppe-tundra conditions.

Differences in pollen spectra from the two stations (e.g., higher percentages of Betula at Station 8) are likely due to distinctions of the former local environments and over-representation of Artemisia. According to macrofossil data (Fig. 12), dwarf birches were definitely present at Cape Deceit during deposition of sediments included in the interval of Sample S-6 (Fig. 9).

j. Deering Formation (Peat 6):

Pollen spectra from Peat 6 at Station 1 and its presumed lateral equivalent at Station 8 show very high percentages of Betula combined with low percentages of Picea and Alnus. An attempt to determine if the birch pollen represents shrub or arboreal birches using criteria established by Birks (1968) was inconclusive.

A pollen sample (72-67, Fig. 10) from blocky, moss peat in the uppermost part of the Cape Deceit exposure differs from Peat 6 spectra by possession of a higher alder percentage, more like the alder values in surface samples. Apparently, when Peat 6 formed around 9,150 years ago, alders were still relatively rare in the Deering area and did not become as common as at present until later in the Holocene.

Discussion of Pollen Data

Environmental interpretations of the Cape Deceit pollen data are summarized in Table 6. Discussed below are comparisons of Cape Deceit data with results of other studies and interpretation of some outstanding features of Cape Deceit.

a. The Imuruk Lake sequence:

Imuruk Lake, south of Deering (Fig. 2), is the site of the most detailed pollen study yet conducted in Alaska (Colinvaux, 1964; Colbaugh, 1968). It is nearer spruce treeline than Deering and alders are more rare there. Also it is at an elevation of 300 m and not as directly influenced by maritime climate as is Deering. Nevertheless proximity of Deering and Imuruk Lake plus the fact that both sites now have a similar regional pollen rain suggest that both might have a similar vegetational history. Thus the Imuruk data play an important part in the following discussion. To facilitate comparison an abbreviated

compilation of Colinvaux's (1964) and Colbaugh's (1968) pollen diagrams is presented in Fig. 11.

Before comparison, several comments on the Imuruk sequence are necessary.

(1) It probably does not represent as much of Pleistocene time as do Cape Deceit sediments. The lake rests on basalts of presumed mid-Pleistocene age (Hopkins, 1963), and the base of the lacustrine sediments was not reached by the longest (8 m) core (Colinvaux, 1964).

(2) I believe that dates for some of the upper zonal boundaries are more uncertain than indicated. Colbaugh (1968) assumes that the Zone J-K boundary is 12,000 years old; however, this date is an average of several C^{14} dates (from different cores) ranging in age from 11,910 to 13,250 years BP. In some cases, such as the C^{14} date for the K-L boundary, the core increment used for C^{14} analysis was as thick as one of the zones to which the date applies.

(3) Not all Imuruk pollen zones are based on the same kinds of data. Samples for Zone M come from an allochthonous peat, representing the shoreline of a former higher level lake, whereas all other samples (except surface samples) are from lacustrine silts and clays. Colbaugh (1968) considered Zone M Intermediate Terrace deposition to have started sometime after 8,620 years and implied that the pollen samples from it represent regional vegetation. I believe, however, that Zone M may be partially correlative with Zone L since C^{14} from some Intermediate Terrace sediments (but not the one from which samples are derived) show that it was forming during deposition of uppermost Zone L sediments (Fig. 11). Zone M pollen samples are from peats; therefore, they are likely biased by local pollen and some of the distinctions between

Zone M and L samples are likely not climatically significant.

(4) I would interpret the lower five meters of the core differently from Colinvaux (1964) (Fig. 11). His correlation results in the Illinoian increment of the core being much shorter than the Wisconsin increment, just the opposite to what is expected if glaciers and associated zones of aeolian deposition were nearer Imuruk during Illinoian than Wisconsin time (Fig. 2).

I agree with Colinvaux that the lower part of the core, in which spruce peaks occur (Zones A-G), is not likely to represent forested conditions at Imuruk; however, I disagree with his contention that these zones represent an interglacial environment essentially like that of the present. The critical point in his interpretation is the significance of spruce peaks in Zones A-G. He considers them to have similar implication as the spruce fluctuations in Zone I and L, but I doubt this because the spruce peaks in the lower zones differ in at least two ways from those above. First, they are not, like the upper spruce peaks, associated with high percentages of alder pollen; therefore, they almost certainly do not represent a shrub tundra environment near treeline as at present. Second, the lower spruce peaks, unlike the upper ones, are associated with zones of sand in the core (not illustrated in Fig. 11. See Colinvaux, 1964). The significance of this fact is not clear, but it could mean that high pollen percentages reflect nothing more than over-representation of allochthonous spruce during a time of very low local pollen production and rapid (aeolian?) sedimentation. Thus, a tundra environment containing dwarf birches, possessing few alders and no spruce may have existed at Deering throughout time represented by Zones A-H. If so, the entire lower five meters of the core,

not just part of Zone G and Zone H, could be of Illinoian age.

b. Comparisons with Cape Deceit Data:

Some of these points concerning the Imuruk sequence become significant when an attempt is made to correlate its pollen spectra with those from the Deering Formation. The case of Peat 6 is a good example, since Colbaugh's (1968) data allow two different interpretations of its probable Imuruk correlative, and my objections as listed above provide still another alternative. (1) If the dates that Colbaugh established for Imuruk zonal boundaries are accepted, then Peat 6 should have formed during Zone L time. Pollen samples from Zone L and Peat 6 differ greatly, notably by the low percentages of spruce and alder in the latter; but as Colinvaux (1967) indicated, such distinctions (or similarities) are not by themselves sound criteria for correlation of Alaskan pollen sequences. (2) C^{14} dates from Core I (Colbaugh, 1968) at Imuruk also allow Peat 6 to be correlated with the upper part of Zone K, samples of which resemble those from Peat 6 by their high content of Betula pollen. (3) Finally, if the base of Zone M is older than Colbaugh has indicated (as I have suggested above) then Peat 6 may have formed during Zone M time.

Until such time as more C^{14} dates from Imuruk and Deering Formation Unit 2 are available, correlation of the Wisconsin and Holocene portions of both sequences will remain as difficult as is indicated in the preceding paragraph. A major problem is that the Wisconsin part of the Cape Deceit sequence is very thin and likely contains several unrecognized unconformities. Possibly the best way to compare it with Imuruk data in the future will be by comparison of both with a Holocene-late Pleistocene lacustrine pollen sequence from Deering or a nearby coastal area.

None of the samples from the upper part of the Deering Formation yields pollen spectra with high spruce values such as those in Zone L at Imuruk, despite the fact that high percentages of Picea in that zone are attributed to westward advance of spruce along the north shore of Seward Peninsula (Colbaugh, 1968; D.M. Hopkins, Pers. Comm., 1969). The explanation for this discrepancy may be that spruce treeline did not, in fact, advance significantly toward Deering during the early Holocene, meaning that high spruce percentages in Imuruk Zone L result instead from allochthonous pollen derived from spruce trees advancing up the valleys south of Imuruk Lake. In this context, it is interesting to note that: (1) the recent conclusion by D.M. Hopkins (Pers. Comm., 1971) that a previous report of spruce fossils in early Holocene sediments around Kotzebue Sound (McCulloch and Hopkins, 1966) is an error, and (2) unpublished pollen spectra by C.S. Schweger (U. of Alberta) which fail to record a peak of spruce pollen in early Holocene sediments at Cape Blossom, near Kotzebue. There is, however, other definite evidence from the Kotzebue Sound area for an early Holocene warm interval. At Cape Deceit this event is probably indicated by slowing deposition of silts and formation of Peat 6.

Arboreal birches expanded west of their present limit during the early Holocene (D.M. Hopkins, Pers. Comm., 1968), which may explain the high percentage of Betula pollen in Peat 6 samples.

Pollen samples from at least the upper part of the clayey silt zone in Unit 2 of the Deering Formation are equivalent in age to those from Imuruk Zone K (Fig. 5, 11), however, many of them differ significantly from Zone K spectra by possession of higher percentages of Artemisia and lower percentages of Betula. The fact that Betula and

Artemisia percentages in the Cape Deceit samples are often negatively correlated shows that the distinctions are probably due to local over-representation of Artemisia pollen. Furthermore, macrofossil evidence shows that dwarf birches were present during deposition of clayey silts at Station 8.

My interpretation of the pollen spectra from clayey silts of Unit 2 differs from that assigned to Zone K spectra. Colinvaux, (1964) and Livingstone (1955) view fossil spectra of the Zone K type as comparable to surface pollen spectra from contemporary birch dominated tundra. But Zone K samples contain higher percentages of both Artemisia and grass than is found in the contemporary shrub birch-tundra pollen rain, meaning that the fossil spectra probably represent a different type of environment--i.e., a steppe-like tundra, albeit one in which birches were more abundant regionally than was the case earlier in Wisconsin time (see Zone J_3 at Imuruk--Fig. 13).

Sediments from immediately below clayey silts at Unit 2 at Cape Deceit contain high percentages of alder pollen, like samples from Imuruk Zone i, and unlike samples from Zone J (Fig. 13). For reasons stated earlier, I believe that the lower part of Deering Formation Unit 2 at Station 8 does correlate with Sangamon Zone i at Imuruk. This, of course, implies that a large part of Wisconsin time is not represented in the sequence at Station 8. Pollen spectra from the basal sediments of Unit 2 at Station 1 (erroneously equated with Peat 5 in Guthrie and Matthews, 1971) are more similar to those from J_2, suggesting that the hiatus is not so great at that part of the exposure. Alternatively, Peat 5 and associated organic sediments with high alder percentages might be equated with a mid-Wisconsin interstadial. But the pollen data from those sediments indicate that spruce treeline was closer to Deering

than at present, while pollen from Imuruk Zone J_2 and the lower part of the Epiguruk exposure on the Kobuk River (Fig. 2; C.S. Schweger, Pers. Comm., 1971) show that spruce treeline during the mid-Wisconsin interstadial was located farther from Deering than at present. Clearly, the assignment of Peat 5 and associated sediments to the Mid-Wisconsin is incompatable with that pollen evidence.

Imuruk Lake and Nome (Colinvaux, 1964; 1967), like Deering, were in tundra during the Sangamon. But forests, including spruce, did occur at Cape Blossom (near Kotzebue, Fig. 2) during Sangamon time (McCulloch, 1967; Matthews and Hopkins, unpublished data). The longitudinal position of Cape Blossom is nearly the same as Deering, so if spruce treeline moved that far west on the north side of Kotzebue Sound why not a similar degree of movement on the south side (placing Deering within treeline)? The question is best answered by reference to present distribution of spruce (Fig. 2), which shows that contemporary climatic warming would result in spruce reaching Kotzebue first from the Kobuk River delta region rather than via a westward migration along the north coast of Kotzebue Sound. With this in mind, it becomes easy to envision Sangamon conditions in which the only spruce growing near the coast of Kotzebue Sound occurred at Kotzebue and perhaps those areas surrounding the most interior portions of the sound, leaving Deering treeless.

Comparison of pre-Sangamon portions of the environmental record at Cape Deceit and Imuruk is difficult, due to problems concerning dating of the pre-Sangamon part of the Imuruk sequence. If Colinvaux's correlations are accepted (Fig. 11), then Deering Formation Unit 1 spectra differ from Illinoian spectra at Imuruk by possession of much lower Artemisia and Betula percentages. However, if the entire lower

portion of the Imuruk core is of Illinoian age, as I have suggested, then pollen records from parts of the sequence are quite similar to Illinoian spectra from Unit 1 (Deering Formation) at Station 8. In both cases, a tundra environment dominated by dwarf birches, but lacking alders, is indicated. Gaps probably exist in the Cape Deceit record since it is a colluvial sequence. No evidence of an unconformity was noted in the upper part of Unit 2 at Station 8, but the greater thickness of Unit 1 loess overlying the "frost crack" zone at other exposures does imply that a hiatus exists immediately below Peat 5 at Station 8. If so, this would explain the absence of spectra similar to those occuring in Illinoian (or uppermost Illinoian) sediments at Imuruk.

Sediments equal in age to the Cape Deceit Formation probably do not occur at Imuruk, and other Alaskan samples with which the Cape Deceit spectra might be compared are rare.

c. Eurasian Evidence:

Pollen studies from eastern Siberia may be profitably compared with those from Cape Deceit, but with caution because the Siberian flora differs from that of Alaska in several important respects and the pollen data are presented in a manner that makes comparison difficult. Pollen and macrofossils from the Olyor-Suite in the Kolymian Lowland imply open tundra with only a few scattered larches, similar to present day conditions in that area (Sher, 1971; A.V. Sher, Pers. Comm., 1970; Katz, et al., 1970). Petrov (1967) suggests that pollen spectra from the Pinakul' deposits (=Alaskan Einahnuhtan) indicate more severe climatic conditions than those at present in Chukotka; however, the basis for this conclusion--domination by Bryales spores--could easily be the result of local over-representation. Correlation of the Chukotkan

Kresta suite (Petrov, 1967) with the established Alaskan sequence is problematical, but according to D.M. Hopkins (Pers. Comm., 1972) it probably includes beds equivalent to both the Kotzebuan transgression and Nome River (Illinoian) glaciation of Alaska. Pollen samples from the upper Kresta subsuite near Svobodny Bay are thought to indicate climatic amelioration like Peat 4 (Petrov, 1967), but the fluctuations recorded in the diagram might be due instead to plant succession on the nearby shoreline rather than climatic change. Marked peaks of Polypodiaceae spores that occur near sedimentary contacts in the 10 m section could result from differential preservation and rebedding--not climatic change.

The Val'katlen sequence of Chukotka is equivalent to the Pelukian transgression (Hopkins, 1972 IN PRESS; Petrov and Khoreva, 1968). As in Sangamon sediments at Cape Deceit, Val'katlen lacustrine deposits, on the north side of the Gulf of Anadyr, record a dominance of alder pollen, which Petrov explains as the effect of more favorable climate that allowed alders to grow on interfluves where at present they do not occur. In Chukotka, however, an alder rich tundra environment also existed during the Amguem interglacial, correlated with the mid-Wisconsin (Petrov, 1967).

d. Artemisia:

Percentages of Artemisia in most tundra spectra from Cape Deceit are higher than in surface samples representing contemporary tundra in Alaska and the northern Northwest Territories (Colinvaux, 1964; Matthews, 1970; Rampton, 1971; Ritchie, 1972; and this paper); however, amounts of Artemisia comparable to those in some samples from the upper part of the Deering Formation do occur in surface samples from the northern Great

Plains of the United States (McAndrews and Wright, 1969). The present distribution of Artemisia in Alaska shows that its occurrence is favored by at least two interrelated factors--deep seasonal thawing and good drainage. Such conditions are not often found in contemporary tundra areas, no doubt explaining the present rarity of Artemisia there.

Continentality of climate has been shown (Yurtsev, 1972) to be the chief limiting factor in the northern distribution of steppe plant communities in Eurasia. The climate of unglaciated Alaska was undoubtedly more continental than at present during times when the Bering Land Bridge was exposed, and the relatively warm, dry summers that probably characterized such a climate would have promoted wider distribution in Alaska of xerophytes such as Artemisia. But other more local conditions--loess deposition or colluvial and alluvial deposition--might also create suitable habitat for Artemisia by inhibiting development of extensive moss and Eriophorum turf, thus prompting deep seasonal thawing and good drainage. If such presently edaphic conditions were widespread during the Pleistocene, they, too, could have caused the high Artemisia percentages found in many fossil samples. Unfortunately, without knowing the Artemisia species represented by the pollen (not a future likelihood according to Praglowski, 1971), it is impossible to know which of the several factors--regional climatic or local depositional--are responsible for high Artemisia percentages. In most cases both probably are, but it is important to remember that local or depositional conditions favoring Artemisia need not have occurred in concert with regional climatic conditions having the same effect. For example, loess deposition might have been greatest shortly before or after maximum exposure of the Bering Land Bridge, and colluvial or alluvial deposition can occur at

any time. Thus, high Artemisia percentages may occur in samples, such as 47-69 (Figs. 7, 10) or those from the Epiguruk interstadial (Kobuk River, C.S. Schweger, Pers. Comm., 1970), which were definitely not deposited in full glacial time when climatic continentality was at a maximum.

III. PLANT MACROFOSSILS

Ecologic and Taxonomic Notes

a. *Larix*:

Abundant seeds, cones and leaves of *Larix* occur in association with or immediately above Peat 1 of the Cape Deceit Formation. *Larix* wood also occurs in Peat 1, as well as at the Cape Deceit-Inmachuk contact. A few poorly preserved seeds, only tentatively identified as *Larix*, but certainly not *Picea*, occurred in the residue of pollen sample 47-69 (above Peat 6--Station 1, Fig. 7).

The best preserved *Larix* cones and seeds are identical to those of *Larix laricina*. I have not examined cones of *L. dahurica* Turcz., an eastern Siberian species, but illustrations and descriptions (Katz, *et al.*, 1965; Komarov, 1934) show that its cones and seeds are very similar to those of *L. laricina*; so even though the *Larix* fossils from Cape Deceit are assigned to *L. laricina*, the possibility that they represent *L. dahurica* instead cannot be ruled out.

Larix wood samples from sediments associated with Peat 1 show evidence of remarkably slow tree growth. Annual increments in one fragment of an overturned stump (15+ cm diameter) had radial dimensions of only 80 microns each. Evidently the trees were growing in a marginal treeline environment, a conclusion substantiated by invertebrate fossils.

b. *Picea*:

Fossils of both white spruce (*P. glauca*) and black spruce (*P. mariana*) occur in Peat 4 samples. A single *Picea* (?) leaf occurs in the S-1 assemblage (Deering Fm., Unit 1), and a well preserved white spruce leaf was found in association with assemblage S 13-67 (Cape Deceit Fm.); yet both assemblages are dominated by tundra fossils. The

spruce leaf from S-1 may have been rebedded from underlying Peat 4 or incorporated in the assemblage during sampling. Excellent preservation of the S 13-67 spruce leaf suggests that it is a recent contaminant.

c. Potamogeton spp.:

Fruits of Potamogeton are abundant in a few samples. I have limited confidence in some of the specific determinations (indicated by "?") because of the great amount of intraspecific variation in some species. Several of the species are known to hybridize, thus contributing to the difficulty of providing specific identifications for fossil Potamogeton fruits.

Pondweeds grow partly or completely submerged and rooted to the bottom. P. perfoliatus usually occurs in deeper water than other species listed in Figure 12. P. filiformis, P. pectinatus, and P. vaginatus are often found in brackish or hard water or in areas with calcareous bedrock (Berglund and Digerfeldt, 1970; Wiggins and Thomas, 1962).

d. Hierochloe:

Sample S-6 (Deering Fm.) contains two florets (with caryopses) of Hierochloe. They are definitely not H. alpina, being instead closest to the other Alaskan species, H. pauciflora, which now grows on tundra near margins of fresh water pools (Hultén, 1968).

e. Poa sp.:

Caryopses of grasses are relatively abundant in assemblage S-6 (Deering Fm., Fig. 12), but only a few of these possess remains of the enclosing lemmas and palaes that provide the most diagnostic characters. Nevertheless, the similarity of naked caryopses to those still bearing lemmas and palaes suggests that they all represent the same genus--

Poa. A specific determination of the better preserved fossils was not possible; however, size of the lemmas and other features show that they do not represent Poa alpigena or P. lanata, two common species of wet or near aquatic sites (Hultén, 1968; Young, 1971; Wiggins and Thomas, 1962). Instead the Poa fossils probably represent one or more of the many species occurring now on mesic or xeric sites.

Most species of Poa are palatable and nurtitious, having high forage value for grazing ungulates (Hitchcock, 1950). With this in mind, note Guthrie's (1968) conclusion concerning the predominance of grazing ungulates in the Alaskan late Pleistocene mammalian fauna.

f. Carex maritima:

Although this species often occurs in association with sandy or gravelly sea-coastal sites (Porsild, 1966; Hulten, 1968), inland localities are also known, Porsild (1966) lists C. maritima ssp. yukonensis as occurring at "calcareous silty places in and around a spruce bog" in the Yukon Territory.

g. Potentilla:

Potentilla achenes are extremely abundant in some samples. They do not represent the bog species P. palustris (=Comarium palustris). Most remaining Alaskan Potentilla species occur on sandy, gravelly soil where vegetation is scattered and grassy (Hultén, 1968). Fossil achenes from assemblage S-6 (Deering Fm.) differ consistently from those in samples S 13-67 and S 11 (Cape Deceit Fm.).

Interpretation and Discussion

Plant macrofossils listed in Figure 12 provide alternate evidence for comparison with paleoenvironmental conclusions based on other data. Included in that figure are fossils from the residue of pollen

samples (see METHODS).

Presence of macrofossils of plants now restricted to forested areas has obvious implication, especially in the case of Picea, since spruce forms present treeline in Alaska. In a few instances, plants now having a boreal distribution in Alaska (e.g., Ranunculus sceleratus, Barbarea orthoceras), occur as fossils in assemblages that otherwise seem to represent former tundra conditions. Identification error may be the fault, or the present distribution of the plant may be poorly known. But also such anomalous assemblages may reflect former tundra environments unlike any known at present (see DISCUSSION; Guthrie, 1968).

a. Forest environments:

Picea glauca, Picea mariana, and Betula papyrifera were all growing at Deering during formation of Peat 4, being further evidence that the peat represents an interglacial. At the time of formation and deposition of Peat 1, larches existed locally in the Deering area, but spruces were apparently absent; for despite an intensive search, no macrofossils of spruce were found in Peat 1 or in the overlying woody sediments. Pollen evidence also implies scarcity of spruce.

Hopkins (1967a, and Pers. Comm., 1968) reports wood of Chamaecyparis (Alaska cedar) from the woody zone immediately above Peat 1. I have been unable to verify the record by collection of Chamaecyparis macrofossils, and unfortunately the originally identified wood specimen has been discarded (D.M. Hopkins, Pers. Comm., 1970). Peat 1 and overlying sediments were deposited in a forest tundra or tundra environment (see INVERTEBRATE FOSSILS), quite unlike the coastal forest environment in which Chamaecyparis nootkatensis (Lamb.), the Alaskan species, now grows. For this reason, I doubt that Chamaecyparis was growing at Deering during Peat 1 time.

A remarkable feature of the 102-69 Peat 1 assemblage (Fig. 12) is the diversity of the Potamogeton flora. At least seven distinct types of fruits are represented. Similar diversity of Potamogeton occurs in the carpological assemblage from the Tiraspolian Olyor Suite in eastern Siberia (Katz, et al., 1970). Few, if any, contemporary tundra ponds in Siberia or Alaska possess a comparable number of Potamogeton species (Johnson et al., 1966; Young, 1971). Perhaps the high diversity in the 102-69 and Olyor assemblages results from the fact that they represent a mixture of fossils from several types of aquatic environments--such as those characterizing a fen-bog successional sequence. The fact that Nuphar (pond lily) and some of the Potamogeton species from 102-69 do not now occur as far west as Deering, is additional evidence for a slightly warmer climate during Peat 1 time.

b. Tundra environments:

Well known regional differences in taxonomic diversity of the contemporary Holarctic tundra flora permit definition of modern tundra zones. It might be possible to apply such a zonation scheme to an analysis of the tundra plant macrofossil assemblages from Cape Deceit.

In contrast with objectively defined physiognomic boundaries, (i.e. northern treeline), boundaries for tundra zones are both more subjective and are based almost entirely on floristic rather than vegetational distinctions. Different floristic criteria may be used for definition of such zones. Palynologists who have worked in Alaska have established tundra zones on the basis of the distribution of alders and dwarf birches (Colinvaux, 1967)--the pragmatic approach since birch and alder pollen are produced in abundance, wind distributed, and easily identified in pollen samples.

A more refined zonation scheme has been proposed by Young (1971). It takes into account many more taxa than used in the palynological system, and floristic differences in regions beyond the limit of alders and birches. Young uses four zones to characterize regional differences of tundra floristic diversity. Zone 1 includes areas with the most depauperate flora (high arctic). Zone 4, including all lowland tundra areas of Alaska, except the northernmost coast and St. Lawrence Island, represents low arctic or hypoarctic tundra adjacent to the boreal forest or taiga. Boundaries of the four tundra zones are correlated with a parameter representing summer warmth. Young's zonation system has predictive value; that is, the climate and flora of a region can be predicted when only a few of the resident plant species are known. It would be fortunate if plant fossil assemblages, which also represent a very small portion of the former flora, could be used in a like fashion to assess the paleofloristics and paleoclimate of a region. To even attempt this, however, specifically identified fossils are required, thus limiting application of Young's data to situations where plant macrofossils are available.

Table 2 lists plant species included in Figure 12 and the tundra zone in which they presently find their northern limit. Note the dominance of low Arctic (Zone 4) species. But many of those listed are submerged aquatics that are sometimes distributed independently of summer warmth. For this reason I hesitate to draw any firm paleoclimatic conclusions. It does seem clear, though, that those units at Cape Deceit which contain identified plant macorfossils were deposited in an environment as floristically diverse and warm as those defined by Young's Zones 3 and 4, representing low to middle arctic tundra. This does not imply vegetational similarity, and in fact, pollen data show that the importance

of such plants as grasses and Artemisia in the former environment must at times have differed greatly from the present.

Pollen samples representing the S 13-67 sample interval (Cape Deceit Fm.) indicate a flora in which alders are either absent or very rare. Alders have their northern limit within Young's Zone 4, but they do not extend as far north as the Zone 4-Zone 3 boundary; consequently, even today, large areas within the limits of low arctic tundra (according to Young's definition) lack alders and might be expected to yield surface pollen samples which, like the fossil samples, contain low alder percentages.

Quantitative data presented in Figure 12 allow comparison of macrofossil assemblages from several stratigraphic units. Cape Deceit Formation assemblages S-11 and S 13-67, and Inmachuk Formation assemblage S-12 are dominated by Potentilla (77-90 percent of total seeds and fruits). Potentilla is also abundant in S-1 from the lower part of the Deering Formation, but that assemblage differs from others by possession of an abundance of Cruciferae seeds. Dominance in the Deering Formation S-6 assemblage is shared by Potentilla, Hippuris, Carex, and Poa. The S-5 assemblage from the base of Deering Formation Unit 2 is distinguished by an abundance of Carex achenes and fungal sclerotia (not tabulated).

Abundance of Potentilla from most assemblages suggests scantily vegetated site conditions substantially different from those prevailing in the immediate Cape Deceit area today. Abundance of Hippuris fossils in Deering Formation assemblage S-6 is undoubtedly related to existence of small ponds (or a thaw lake basin) at Cape Deceit. Almost 18 percent of fossils in assemblage S-6 are of Poa; however, this cannot be due to local aquatic conditions (as is the Hippuris frequency), since the Poa species represented by fossils are not those now common to aquatic or

shoreline habitats (see Ecologic and Taxonomic Notes). Instead, abundance of Poa fossils probably reflects regional environmental conditions and possibly indicates that the Deering region was more akin to a grassland 12,400 years ago (when S-6 was deposited) than it is at present. Fossil insect and pollen data support this conclusion.

IV. INVERTEBRATE FOSSILS

Table 3 and Figure 14 list fossil Arthropoda and Mollusca collected at Cape Deceit. Fossils of Coleoptera (beetles) dominate. Figure 14 includes fossils from the residues of pollen samples. Table 3, on the other hand, lists assemblages of fossils picked from the sieved residue of peat samples and large volume silt samples. Quantitative documentation is provided for some of the assemblages by tabulating the minimum number of individual insects represented by the fossils (Matthews, 1968). The total number of insects represented by each assemblage so documented and the amount of sediment processed is given in Table 4. It shows that caution must be used in interpretation of inter-assemblage differences of quantitative abundance or taxonomic diversity (Table 3), since variable sample size is no doubt partly responsible for such distinctions. For example, note in Tables 3 and 4 the difference in taxonomic diversity and sample size (revealed by the number of individual insects) in S-12 (Inmachuk Fm.) and S-6 (Deering Fm.).

Table 3 also includes information on the distribution and habitat requirements of certain taxa. Sources for this information are published notes (chiefly in the works of C.H. Lindroth), locality information on museum specimens that I have examined, and my own and others' collecting notes. See Table 3 for ecological information on taxa listed in Figure 14. Stratigraphic position of all samples listed in Table 3 and Figure 14 is given in Figure 7.

Ecologic and Taxonomic Notes

a. Homoptera:

Fossils of leafhoppers (Cicadellidae) are relatively abundant

in some of the assemblages. Most species feed on grasses. Athysanella is chiefly associated with the "short grasses" (Ball and Beamer, 1940). The genus is not known from Alaska today and except for a few records from relict grassland areas in the Northwest Territories and northern British Columbia, it is found only in extensive grassland regions such as the western Canadian prairies (Beirne, 1956; K.G.A. Hamilton, Pers. Comm., 1970).

The leafhopper genera Sorhoanus, Perdanus, and Psammotettis, individuals of which are common in contemporary grassy tundra areas of Alaska (Hamilton, Pers. Comm., 1970), are not represented in any of the fossil assemblages. While not implying their absence from the former insect fauna, this fact does strongly suggest (particularly in the case of assemblages containing large numbers of fossils--e.g., S-6) that individuals representing these three genera were at times during the Pleistocene less common than those of other leafhopper taxa which are rare (maybe absent) in contemporary tundra regions.

Like Athysanella, the fulgorid genus Aphelonema is characteristic of prairie areas, with a few specimens having been taken in northern relict grasslands--not in Alaska, however (Hamilton, Pers. Comm., 1970). Neither is the psyllid Trioza quadripunctata Crawford a member of the contemporary Alaskan fauna. It occurs on species of nettle (Urtica) Tuthill, 1943), but none of the three species of Urtica, which now grow in Alaska, has been recorded from lowland tundra areas (Hultén, 1968).

b. Pterostichus nearcticus Lth. (Fig. 15 C)

The single pronotum referred to this species was compared with the holotype in the Canadian National Collection (Ottawa). P. nearcticus is presently known only from the islands of the Anderson River Delta

(northern Northwest Territories). A glacial refugium has been postulated for that area because, in addition to P. nearcticus, the species Pterostichus stantonensis Ball and morphologically distinct populations of other species occur only there (Ball, 1966). But since P. nearcticus occurred in western Alaska during the late Wisconsin, its present restriction to the Anderson River Delta can hardly be an indication of refugial endemism.

In the Anderson River area P. nearcticus is found on "sandy soil with open grassy vegetation" (Lindroth, 1966). Perhaps the prevalence of grassland conditions in late Pleistocene Alaska (Guthrie, 1968; Matthews, unpublished manuscript; and this paper) explains the former more cosmopolitan distribution of this species.

Other species of the subgenus Derus, to which P. nearcticus belongs, occur in Siberia. In view of the late Wisconsin record of P. nearcticus at Deering, it would not be surprising if that species were also to occur in late Pleistocene fossil assemblages from Siberia. Sediments of the Siberian middle Pleistocene Olyor Suite contain several fossils referred to the subgenus Derus, but none of these is P. nearcticus.

c. Subgenus Cryobius:

Fossils of ground beetles of the subgenus Cryobius (genus Pterostichus)are usually abundant in Alaskan fossil insect assemblages, especially those representing treeless environments (Matthews, 1968 and unpublished material). Some species within the subgenus can be identified reliably only by reference to the male genitalia, which makes identification of fossils especially difficult. But, most of the commonly encountered species--P. (Cryobius) nivalis, P. (Cryobius)

brevicornis, P. (Cryobius) ventricosus, P. (Cryobius) similis, P. (Cryobius) parasimilis, P. (Cryobius) kotzebuei, and P. (Cryobius) tareumiut--can usually be distinguished on the basis of pronotal characters alone.

The latest phase of Cryobius speciation almost certainly antedates the Wisconsin (Ball, 1969; Matthews, 1968), making Cryobius fossils of middle and early Pleistocene age potentially valuable for documentation of evolution in the group. Both Cape Deceit and Inmachuk formations contain such fossils.

Five species of Cryobius (tareumiut, similis, pinguedineus, ventricosus, and mandibularoides) are represented in Cape Deceit Formation assemblages by fossils including the diagnostic male genitalia (Table 3).

Identifications of P. (Cryobius) tiliaceoradix and P. (Cryobius) biocryus are also based on presence of male genitalia, but nevertheless are considered tentative (Table 3) because of the uncertain status of some species within the planus group (to which tiliaceoradix and biocryus belong) and the fact that I have seen only one male specimen of biocryus (NEW RECORD, Alpine Interior Alaska, det., G.E. Ball).

The P. (Cryobius) nivalis record from Peat 1 is based on a well preserved partially articulated specimen (lacking genitalia). Another partially articulated fossil, P. cf nivalis (Table 3), possesses male genitalia slightly different from those in typical nivalis; however, the difference may be only a preservation artifact. P. (Cryobius) auriga and P. (Cryobius) kotzebuei also occur in the Cape Deceit Formation, but the distinctive male genitalia of the former species are first recognized in sediments of the overlying Inmachuk Formation (Table 3, S-12).

Two male median genital lobes of P. (Cryobius) similis from the S 13-67 assemblage (Cape Deceit Fm.) are confirmation that similis had evolved by late early Pleistocene time. Both these fossils match anomalous similus genitalia, which Ball (1966) and I have noted in a few contemporary specimens. Ball has suggested the possibility that the contemporary anomalous specimens are similis X tareumiut hybrids. But this is improbable in the light of S 13-67 fossils since it is unlikely that hybridization of two sympatric species would take place over such a long period (400,000+ years) without occurrence of either (1) genetic swamping (through introgression) of one parental stock by the other or (2) divergent selection leading to complete interspecific genetic incompatiability. The aberrant similis males in contemporary populations might mean that similis is dimorphic in certain genital characters, as is apparently the case for another carabid, Harpalus amputatus (Ball, Pers. Comm., 1971). Or, alternatively, they may indicate that similis, as currently defined, includes two species.

Hand collecting and pitfall trapping of insects were carried out at Deering with the hope of gaining more detailed information on habitat requirements of Cryobius species. The following species occur there: P. brevicornis, P. tereumiut, P. parasimilis, P. similis, P. kotzebuei, P. pinguedineus, P. ventricosus, and P. mandibularoides. P. nivalis, though not collected by me, probably occurs in the Deering region and P. byrantoides, heretofore known only from the Alaskan-Yukon border (Ball, 1966), is now also known from Kotzebue (Fig. 2).

P. brevicornis specimens were common only at disturbed sites near the village. P. soperi was rare at Deering, and like P. brevicornis, was not collected at undisturbed tundra sites. But I have collected soperi in alpine interior Alaska where vegetation cover is thin and

sparse, this possibly being its preferred habitat. All remaining species of Cryobius that occur at Deering, except similis, seem to be perfectly sympatric with few evident differences in habitat requirements. P. tareumiut and P. parasimilis were abundant in most pitfall traps located in areas of thick continuous turf cover. They were absent and similis was abundant in traps located where vegetation cover was sporadic.

d. Harpalus amputatus Say:

This species is common in grassland areas of western North America (Lindroth, 1968). Contemporary specimens have been collected at only two Alaskan sites and neither of these is in a tundra region; however, the species did occur in interior (Table 5) and western Alaska during the late Pleistocene, a time when those two areas possessed a periglacial, treeless environment (Matthews, 1968, 1970; and this paper).

e. Neoscutopterus cf horni Lec.:

Peat 1 and Peat 2 contain partially articulated fossils that are very near if not conspecific with the dytiscid beetle Neoscutopterus horni Lec. This species now occurs as far west as Nome, Alaska and is found in the cold water of Carex-Sphagnum bogs, usually where the water is shaded by willows or spruces (D. Larson, Pers. Comm., 1971).

f. Subhaida sp. (Fig. 15 F):

Abundant well preserved fossils of a small omaliine staphylinid, belonging to the tribe Corphiini, occur in assemblage S-1 from the Deering Formation. The generic identity of the specimens is not definitely established, but they have been compared with examples of several Corphiini genera (Boreaphilus, Ephelinus, Occiphelinus, Coryphium, Pseudohaida, Subhaida) and found to be similar to Subhaida, a monotypic genus (S. rainieri Hatch) from the Pacific Northwest (Hatch, 1957). If the generic identification of S-1 fossils is correct, they

must represent an undescribed species.

g. Micralymma brevilingue Schiødt.:

Steel (1958, 1961) recognizes three species of Micralymma, two of which, M. brevilingue Schiødt. and M. marinum (Strøm), occur in northern North America. Fossils from the Cape Deceit sequence can be reliably referred to the former, and features of the heads show that all probably represent the subspecies dicksoni Makl., which now occurs in arctic areas of northwestern North America and Siberia. M. brevilingue has not been collected at Deering, but probably occurs there since it has been recorded from other areas around the Bering Sea and Chukchi Sea (Steel, 1958).

Although not restricted to the intertidal zone like M. marinum, M. brevilingue is nevertheless primarily a coastal species (Steel, 1958). In contrast, its past distribution has been pronouncedly non-coastal. Deering was far inland 12,400 years ago (see position of -30m shoreline, Fig. 2; Hopkins, 1967a) when sediments yielding the S-6 assemblage were deposited, and possibly as well during deposition of most other sediments containing Micralymma fossils.

Deering has had a coastal location intermittently during the Pleistocene suggesting that one possible explanation for the former inland occurrence of Micralymma is survival of relict coastal populations following the retreat of shoreline due to sealevel lowering. But Micralymma fossils also occur in late Pleistocene sediments from interior Alaska (Table 5; Matthews, 1968), an area never near marine shoreline during the late Cenozoic. Thus a more likely explanation of the past noncoastal distribution of Micralymma brevilingue is that it reflects features of the former environment which are duplicated currently only in coastal areas. Further discussion of this conclusion is given below.

h. Tachinus apterus Makl.:

Fragments of this staphylinid beetle are extremely abundant in several of the fossil insect assemblages (S-6, S 10-67, etc.--Table 3). Their specific identity is established by inclusion in the assemblages of partly articulated specimens possessing, in some cases, the diagnostic terminal abdominal segments.

Figure 17 presents data on elytral dimensions of T. apterus fossils from several of the samples (assemblages) listed in Table 3. Also shown in Figure 17 are wings of two contemporary T. apterus specimens and a left wing that was found folded beneath a T. apterus elytron in the S 10-67 (Cape Deceit Fm.) assemblage. Even though the fossil wing is incomplete, several features suggest that its apical margin was approximately as I have shown. (1) The length of the stigma (st.) and the distance between the anterior margin of the stigma and the wing base is less than in specimens of fully winged species similar in size to T. apterus. (2) Neither in the illustrated, unfolded wing or in other still folded fossil wings from the Cape Deceit Formation is there evidence for appreciable wing membrane posterior to the position of the stigma. (3) Unlike the situation in contemporary full-winged Tachinus species, the apex of the fossil wing (when folded) did not rest beneath the opposite elytron. (4) Very weak development of viens posterior of the stigma in the fossil contrasts with the condition of wings in specimens of full-winged species.

Evidently, the fossil wing was non-functional, in as much as it is shorter and less developed apically than wings in specimens of present day full-winged species. However, it is considerably larger than wings in contemporary specimens of T. apterus. They are similar in size to the two wings illustrated in Figure 17. I have seen no

long winged specimens of T. apterus (48 specimens--Siberia, Alaska, Yukon Territory), implying that it is not a wing dimorphic species; but as Chiolino (1970, and Pers. Comm., 1972) points out, a much larger sample than 48 specimens, or evidence of reduced mesonota (not the case for T. apterus) is required before a definite statement on wing dimorphism can be made. It T. apterus is not now wing dimorphic and was not in the past, than the difference in size between the fossil and contemporary wings represents the amount of wing reduction that has occurred during the last 400,000-600,000 years. According to Figure 17, evolution of smaller wings was accompanied by changes in elytral proportions. Older fossil elytra are relatively longer with respect to width than elytra of late Pleistocene (Assemblage S-6) and living specimens.

T. apterus is a tundra animal, but otherwise little is known of its ecologic requirements. Like some other Tachinus species, it may be associated with decaying vegetal or animal matter. Its inability to fly means that it is certainly not an obligate dung feeder, since a prerequisite of scatophagy is an effective means of dispersal.

i. Morychus aeneolus (Lec.): Fig. 15 G

Fossils that probably represent this species of byrrhid beetles are abundant in the assemblage of sample S-6 (Fig. 7, Table 3), but the environmental significance of this fact is obscure since very little is known of the ecological requirements of M. aeneolus or other North American species. W.J. Brown reports (Pers. Comm., 1971) collecting M. aeneolus in a grass lawn in the north. I have one specimen of M. aeneolus (?) from scantily vegetated silts on the floodplain of an Alaskan river, and the Palaearctic species M. dovrensis Munst. is reported from a similar type of habitat (Andersen, 1968). The same

sort of local conditions may have existed at Cape Deceit 12,400 years ago, explaining the abundance of Morychus fossils in S-6. On the other hand, other data associated with the S-6 assemblage suggest that the regional environment at that time differed significantly from that of present day tundra or forested regions of Alaska. If so, the abundance of Morychus fossils may mean that pill beetles of that genus were actually more common and widely distributed during the late Wisconsin than at present. Their present rarity could be due to the near elimination, during the Holocene, of their preferred habitat.

j. Chrysolina spp: Fig. 16.

Figure 16 includes illustrations of several fossil genitalia (median lobes) which almost certainly belong to Chrysolina, but match none of those from the known North American species (Brown, 1962). Median lobes illustrated in Figures 16b and 16c are similar to those seen in members of the Chrysolina rufilabris Fald. species complex (Kontkanen, 1959; Fig. 16d). The specimen illustrated in Figure 16a possesses a sinuation of the upper margins, suggesting that it, like the Nearctic species C. cavigera Sahlb. and the Palaearctic species, C. sylvatica Gebl. and C. subcostata Gebl., once possessed dorsal-lateral sclerotized plates (Brown, 1962; Kontkanen, 1959).

The fossil assemblage from S-6 also includes a number of Chrysolina pronota (Chrysolina sp. A, Table 3) which differ from pronota in all Nearctic and Holarctic species by their relative breadth, protruding hind angles, and slightly sinuate sides. They likely represent one of the species in the complex contemporary Chrysolina fauna of the Palaearctic.

k. Lepidophorus lineaticollis Kirby:

Individuals of this phytophagous weevil species occur at xeric sites within forest and tundra regions. In the latter I have collected them only where vegetation cover is sparse (e.g., Dryas fell-field), but this is no doubt due to the fact that in today's sedge-moss dominated tundra only such sites are sufficiently dry. Abundance of L. lineaticollis in fossil assemblages does not necessarily indicate former fellfield conditions, since a drier, grassy tundra than exists at present might also satisfy its habitat requirements.

1. Vitavitus thulius Kissinger:

This species of weevils is currently very rare, being known only from a single specimen taken at Bernard Harbour, NWT (Kissinger, MS 1972), but judging from the number of V. thulius fossils in the assemblage from S 10-67 (Table 3), this may not always have been the case. V. thulius also occurs in Pliocene sediments from Alaska as well as in Pleistocene sediments from the Yukon Territory and Alberta (Matthews, unpublished data).

m. Diptera:

The genus Xylophagus (Xylophagidae) is represented at Cape Deceit by the distinctive caudel plates of the larvae. Some of these are identical to caudel plates from the last instar larvae of X. abdominalis Loew, the only species of the genus with a far northern distribution (Leonard, 1930).

The puparium of Meoneura (Milichidae) in assemblage S-12 may not be a fossil. It is exceptionally well preserved and a contemporary Alaskan species, M. lamellata Collin, is known to inhabit swallow nests (Cole, 1969) which are abundant in parts of the Cape Deceit exposure (see remnant of swallow tunnel in Fig. 6D).

n. Formididae (Hymenoptera):

A more boreal ant than Camponotus herculeanus (L.), could hardly be found (Gregg, 1963). Fossils of that species in Peat 4 are good evidence for the presence of trees, chiefly conifers, and also imply good drainage since C. herculeanus requires dry nesting sites (Sanders, 1964).

Leptothorax canadensis Prov. (Fig. 15E) also occurs in Peat 4 and the organic silts associated with Peat 5 (Fig. 6E; Fig. 14, sample 99-68). Fossils of L. canadensis are not a definite indicator of forested conditions since the species has been collected in alpine tundra, barely beyond the limit of trees (Gregg, 1963), and on tundra at Umiat, north of the Brooks range in Alaska (L. acervorum canadensis Prov., Weber, 1948). I did not succeed in collecting L. canadensis at Deering and rather doubt that it occurs there now. If this assumption is correct, then sample 99-68 and others containing L. canadensis were probably deposited when treeline was closer to Deering than at present.

o. Hymenoptera other than Formicidae:

Most fossils, consisting chiefly of heads and propodea, could be identified only to the tribal or generic level (W.R.M. Mason, Pers. Comm., 1972). Species of the Eurytoma gigantea group (Chalcidae) (S 13-67, Table 3) are not presently known to occur north of Alberta or British Columbia (Mason, Pers. Comm., 1972). Similarly, the present distribution of the ichneumonid genus Anomalon (S-6, Table 3) is chiefly tropical and warm temperate, while a few species occur in dry areas of interior British Columbia and south Alberta. Seward peninsula was definitely not warmer when Eurytoma gigantea and Anomalon existed there, but the tundra at that time may well have been drier and in other respects

different from present day tundra. This might explain the fact that Cape Deceit fossil assemblages containing an abundance of inchneumonid fossils do not include representatives of the subfamilies Tryphoninae and Mesoleiinae--both of which are well represented in contemporary shrub tundra areas of Alaska (W.R.M. Mason, Pers. Comm., 1972).

A few fossils from the S-1 Deering Formation assemblage were exceptionally well preserved as a result of having been cemented together in silt peds. In one case--undoubtedly a host-parasite association--fossils representing several specimens of the parasitic wasp Macrocentris (Braconidae) were found with fragments of the head capsule of a lepidopteran larva--the probable host.

p. Tarentula pictilis (Emerton): Fig. 15 J

The male palpus provides the most diagnostic characters for specific identification of many spiders, but only rarely is such a small and complex organ preserved as a fossil (Leech and Matthews, 1971). One such case is the palpus of Tarentula pictilis (ident. by R. Leech, Ottawa) from fossil assemblage S-5. T. pictilis has not been recorded from Alaska but is known to occur in other subarctic areas of North America (R. Leech, Pers. Comm., 1971). Individuals of T. pictilis are pronounced heliophiles and can often be found at relatively dry sites.

q. Lepidurus sp:

Mandibles of the tadpole shrimp Lepidurus occur in many assemblages, but by themselves are not sufficiently diagnostic for specific determination; however, they probably represent the contemporary northern species L. arcticus Pal. Notostraca (tadpole shrimp) inhabit small ponds, usually those which are too seasonal or ephemeral to support fish.

Interpretation

Insects are much less vagile than most pollen; therefore, it might be expected that their fossils would provide information chiefly pertaining to the former local environment. Unlike pollen, however, many insect fossils can be specifically identified, allowing inferences to be made on the basis of what is known of their present distribution. Many species listed in Table 3 are restricted to certain types of regional environments, e.g., tundra, boreal forest, grassland, etc., or special types of local habitat (ponds, marshes, etc.). Fossils of ground beetles (Carabidae) are most useful for paleoenvironmental analysis because their distribution is predominantly a function of regional or macro-climatological conditions.

Use of fossil data for paleoenvironmental reconstruction is dependent on one major assumption--that ecological requirements of a species do not change through time (Coope, 1967). Under such an assumption a marked difference in the former distribution of an insect species, compared with its present range, will be interpreted as evidence of environmental change rather than change of the species' habitat requirements.

Insect assemblages from samples listed in Table 3 are biased by the fact that they represent almost only the terricolous portion of the former fauna, and of that, chiefly the fraction containing heavily sclerotized insects, e.g. Coleoptera. This explains the rarity of fossils of Diptera and Collembola, both of which are dominant in most contemporary tundra faunas (Hurd, 1958; Watson, et al., 1966).

The environmental implications of the invertebrate assemblages listed in Table 3 and Figure 14 are discussed in the following paragraphs.

a. Cape Deceit Formation (Unit 1):

Two arthropod assemblages (samples D-1 and S-11, Table 3, Fig. 7) from this unit contain mostly taxa that have obligate or facultative tundra affinities. This supports pollen evidence of tundra conditions. Unfortunately, no macrofossil evidence is available for pollen sample 79-68 which implies presence of spruces in the Deering area early in Unit 1 time.

A few fragmented fossils of aquatic gastropods occurred within the sandy-silts of sample D-1, (Fig. 14), but they are probably allochthonous or rebedded, for the D-1 assemblage contains no fossils of aquatic insects.

b. Cape Deceit Formation (Peat 1):

Pollen data from Peat 1 might be misconstrued as evidence of larch dominated forests in the Deering area. Contradicting such an assumption is the occurrence in the Peat 1 arthropod assemblage (Table 3) of such typically tundra species as Carabus truncaticollis and others, like Elaphrus lapponicus, which now barely occur beyond or above treeline (Lindroth, 1961). Instead of forests, the Deering area during Peat 1 time, must have possessed a forest-tundra type of environment in which larches were restricted to small groves. In other words, treeline, formed of larches, existed near what is now Deering.

c. Cape Deceit Formation (Unit 2):

Of the two assemblages representing this unit, only the one from S 10-67 is documented quantitatively. The assemblage from S 13-67, at another part of the exposure (Fig. 7) contains many taxa in common with S 10-67 and is similarly characterized by dominance of Tachinus apterus, Vitavitus thulius, and Ceutorhynchus. T. apterus fossils also occur in the residue of some of the Unit 2 pollen samples (Fig. 14),

indicating that their abundance in assemblage S 10-67 is not an anomaly but instead a characteristic of the entire sedimentary unit.

All specifically identified fossils from S 13-67 and S 10-67 represent obligate or facultative tundra animals. A tundra environment is clearly indicated. Moreoverm the abundance of Amara alpina suggests a mesic to xeric local environment (Schmoller, 1971; Lindroth, 1968).

d. Inmachuk Formation:

This unit is represented by one large fossil assemblage (S-12, Table 3) and a few fossils from the residue of pollen samples (Fig. 14). The S-12 sample interval includes some of the disturbed silts at the top of the unit, but none of the organic sediments of Peat 3.

Predominance of fossils of obligate tundra insects in the S-12 assemblage is indicative of former tundra conditions. Moreover, the high proportion of Amara alpina fossils implies a xeric to mesic local environment, which may, in turn, account for the paucity of Cryobius fossils (see also assemblage S-1, Deering Fm.). In contrast to the S 10-67 assemblage (Cape Deceit Fm.), and like other insect assemblages from younger portions of the sedimentary sequence, the one from S-12 contains an abundance of leafhopper fossils (Table 3), all of which are assigned to the genus Deltocephalus. But without specific identifications, the significance of this fact is difficult to determine. It probably implies local abundance of grasses, but not all species of Deltocephalus are grass feeders (Kramer, 1971).

Despite evidence for a mesic to xeric local environment, the assemblage from S-12 and pollen sample residues from the Inmachuk Formation include a few fossils of aquatic animals (Colymbetes, Donacia, Lepidurus, Daphnia, ostracods, etc.--Table 3, Fig. 14) and a single fossil of the aquatic plant Zannichellia palustris (Fig. 12). Evidently,

small ephemeral ponds existed near Cape Deceit during S-12 time even though the local environment (and perhaps the regional environment) was dry. The possibility that these aquatic fossils indicate presence of a thaw lake (commonest type of lake in permafrost areas) is ruled out by the fact that such fossils are relatively rare in the assemblage (Table 3) and sediments of the Inmachuk Formation (except Peat 3) are relatively inorganic (Table 4).

e. Inmachuk Formation (Peat 3):

A fossil of Amara alpina, from the residue of pollen sample 94-68, (Fig. 14), shows Peat 3 also formed in a tundra environment, as indicated by pollen evidence (Fig. 8).

f. Deering Formation (Peat 4):

Occurrence in this assemblage of fossils of Camponotus herculeanus, Pterostichus hudsonicus, and Leptothorax canadensis indicates that trees existed in the Deering region. The assemblage also includes a well preserved articulated specimen (male with genitalia) of the tundra beetle, Pterostichus parasimilis (Table 3): so in spite of the presence of trees, some open sites suitable for survival of tundra insects must have existed in the area.

g. Deering Formation (Unit 1):

Assemblage S-1 comes from the henseli Zone at the base of Deering Formation Unit 1 (Fig. 7). Like the pollen spectra from this zone, the insect fossils clearly indicate former tundra conditions. In several respects the S-1 assemblage resembles S-12 from the Inmachuk Formation. For example, Amara alpina is the dominant member of the carabid portion of the assemblage, fossils of the leafhopper Deltocephalus are abundant, and Cryobius fossils are rare. Like the S-12 assemblage, S-1 probably also represents a mesic to xeric, grassy local environment.

The manner in which some fossils are preserved supports this conclusion and helps explain peculiar features of this and other assemblages. A few articulated fossils from the S-1 assemblage occurred in calcareous-cemented silt peds. In one case braconid wasps (Macrocentris) and their lepidopteran host were found cemented together. A host-parasite association such as this is especially ephemeral and the fact that evidence of it is preserved at all must mean that carbonate cementation of peds took place near the soil surface shortly after death of the animals. This could not occur in the acidic soils typical of present day tundra; therefore, during S-1 time soil pH values at Deering were probably high--perhaps more like those of contemporary grassland or steppe regions. Calcareous cemented peds occur in other samples as well (notably S-12), but only in sample S-1 were they found to contain insect fossils.

Of all the assemblages, S-1 contains the greatest proportion of Micralymma brevilingue individuals (17 percent of the total, Tables 3, 4). The present coastal distribution of this species suggests that its most critical ecologic requirement may be a substrate possessing a high concentration of mineral salts. Such conditions that would likely have existed at Deering during S-1 time if, as suggested above, soil pH values were significantly higher than at present. Thus, the very factors possibly responsible for lower soil acidity--arid climate, absence of mosses--might also create conditions allowing M. brevilingue to exist at sites other than coastal ones. Occurrence of Micralymma in other assemblages and in late Pleistocene interior Alaska (Matthews, 1968; Table 5) may have a similar explantion. As indicated earlier and below, a steppe-like environment existed at Deering late in Wisconsin time during deposition of sample S-6. In such an environment substrate

pH would certainly have been higher than in contemporary moss-sedge dominated tundra. Grassy tundra may have prevailed regionally during deposition of both S-1 and S-12 (Table 3), but just as significant perhaps is that the local Cape Deceit area at those times was characterized by deposition of slightly leached or unleached silts in a scantily vegetated environment. At all times when Micralymma was present, mosses such as Sphagnum were probably rare. In contrast, S-5 which contains fossils indicative of deposition in a moss rich tundra such as that of the present, has no Micralymma fossils. Micralymma does occur in Peat 1, but it formed at a time when sea level may have stood near its present elevation. And moreover, Peat 1 is not an acid peat, since it contains numerous fossils of Larix--a calciphile (Hultén, 1968).

h. Deering Formation (Unit 1, "frost crack" zone):

No sediments in the entire Cape Deceit sequence are as inorganic as those in the upper part of Unit 1. For example, a 350 kg sample of these silts yielded, upon sieving, only ½ liter of organic residue, most of which consisted of filamentous plant fragments rather than seeds or insect fossils. The few insect fossils which are in the "frost crack" zone (S-7, Table 3) indicate deposition in a treeless environment. Moreover the fossils are well preserved and possess no evidence of pitting or bleaching, common features of insect fossils from highly weathered sediments. Thus, the inorganic character of Unit 1 sediments is likely a primary feature and not the result of post-depositional degradation.

i. Deering Formation (Peat 5):

In Table 3 fossils referred to Peat 5 are from the nodular peat seen in Fig. 6E. Though the sample is small they confirm that the peat formed in a tundra environment. Leptothorax canadensis, a fossil of which occurs in organic sediments immediately above the peat (Fig. 14),

implies that treeline was somewhat closer to Deering than at present; however, in this particular case, the best evidence for this is the pollen data.

Assemblage S-5 also comes from the organic peaty sediments at the base of Unit 2, and therefore, like Peat 5 and associated sediments nearby, probably represents the last (Sangamon) interglacial. S-5 differs in several ways from the other quantitatively documented assemblages (Table 3). For example, in it fossils of Pterostichus parasimilis, a species now common at Deering, are abundant. The same applies for fossils of P. nivalis--indicating thick turf cover and abundance of mosses, as in the present tundra environment. However, some open, unvegetated sites must have existed during deposition of S-5 in order to account for presence of Chiloxanthus stellatus, Tarentula, and Lepidophorus lineaticollis. Such areas were likely not extensive and probably differed little from the small bare silt areas associated with peat rings and other congeliturbation phenomena in present day tundra at Cape Deceit.

j. Deering Formation (upper Unit 2):

Assemblage S-6 is from the clayey silts in the upper part of Unit 2. Wood from the sample interval is dated at 12,400 years BP; therefore, the assemblage is approximately of the same age as the -38 m shoreline in Kotzebue Sound (Creager and McManus, 1967; Hopkins, 1972 IN PRESS, Fig. 2). The assemblage includes fossils of aquatic animals (i.e., corixids, Helophorus, dytiscid beetles, ostracods and Lepidurus), but they form only a small part of the assemblage compared to fossils of insects representing mesic to xeric treeless conditions (i.e., Amara alpina, Trichocellus mannerheimi, Lepidophorus lineaticollis, etc.). That the former environment was more steppe-like than contemporary

tundra is indicated by fossils of grassland insects such as Athysanella, Aphelomena, Harpalus amputatus, and possibly Pterostichus nearcticus. Dominance of the Cryobius portion of the assemblage by Pterostichus soperi probably means that the site was scantily vegetated (See Taxonomic and Ecologic Notes), and further evidence of this fact is the abundance of Morychus and Lepidophorus lineaticollis fossils.

Comparison With Other Studies

Paleoenvironmental studies using fossil insects are new to North America, but not to England where research of this type has been carried on for over a decade (see Coope, 1970, for a review). But the great distance between Great Britain and Alaska, latitudinal differences, and the disparity of their contemporary faunas, largely preclude comparison of Alaskan and British studies.

A series of insect assemblages from Eva Creek in interior Alaska provides about the only information with which data presented here can be compared (Matthews, 1968). Since 1968, the list of fossils from Eva Creek has been updated, and a revised version is presented in Table 5. Note that Harpalus amputatus and Micralymma brevilingue are represented. Some of the Eva assemblages, especially Eva 3-3C (Matthews, 1968), possess a great number of Lepidophorus lineaticollis fossils like the S-6 assemblage from the Deering Formation. Lepidophorus lineaticollis and Morychus are even more abundant in an unpublished assemblage from latest Wisconsin sediments at Fairbanks (Eva 3-3D, Matthews, 1970), and pollen spectra from those sediments, like spectra associated with S-6, contain relatively high percentages of grass (Matthews, 1970).

Through the kindness of A.V. Sher (Museum of Paleontology, Acad. of Sciences, U.S.S.R.), I have had the opportunity to examine a few

small fossil insect assemblages from the Tiraspolian Olyor sediments in eastern Siberia. As with Cape Deceit assemblage S-6 (Deering Fm.), several of the Siberian assemblages contain an abundance of Morychus fossils; however, Lepidophorus is absent. The subgenus Derus, to which Pterostichus nearcticus belongs, is represented by several fossils, none of which are from nearcticus. Trichocellus mannerheimi occurs in some of the assemblages, showing that it had evolved by middle Pleistocene time. Finally, fossils of both Amara alpina and its sister species Amara bokeri occur in the Tiraspolian Siberian sediments as they do in Cape Deceit Formation sediments, providing furthur confirmation that these two species evolved from a common ancestor before middle Pleistocene time.

DISCUSSION

The object of this study is to document Quaternary environmental change in the Deering-Cape Deceit area (Table 6 for summary), and to infer, when possible, paleoenvironmental conditions in the larger Seward Peninsula region. Fossils from any one time period within the Cape Deceit sequence represent part of a formerly functioning ecosystem. Moreover, since most of the fossil evidence presented here relates directly or indirectly to tundra environments, this paper is in reality a partial record of the evolution of the tundra ecosystems at Deering.

Ecosystem evolution is defined here as a long term shift in composition and dynamics of an ecosystem due ultimately to climatic change. This study shows only changes in composition. That these involved some changes in the dynamics of the system is inferred.

Changes in the biotic portion of the system occur in two ways: (1) In situ evolution of plant and animal taxa within the system--"phyletic ecosystem evolution"; and (2) Shifts in the relative abundance of taxa already existing within the system or substitution by taxa from other contemporaneously functioning ecosystems--"non-phyletic ecosystem evolution".

I. PHYLETIC ECOSYSTEM EVOLUTION

Phyletic ecosystem evolution at Cape Deceit is illustrated by changes in the Predicrostonyx-Dicrostonyx small mammal linage of microtine rodents (Guthrie and Matthews, 1971)--presumably a response to changing tundra conditions during the last 400,000-600,000 years.

Cape Deceit fossils provide no evidence of in situ plant evolution. But neither do the assemblages listed in Figure 12 include many fossils of leaves or floral parts, which are required in order to document evolution (if any) among existing groups of closely related

species--those most likely to have undergone some evolutionary change during the time span of Cape Deceit deposition. Lack of specific determinations for many of the plant fossils that are listed in Figure 12 and in the pollen diagrams also hinders assessment of possible plant evolution.

An abundance of identifiable insect fossils from Cape Deceit provides a sounder basis for assessment of the part insects have played in phyletic ecosystem evolution. Most fossils that could be identified to species are referred to extant species, and those listed as being near (cf) a contemporary species may just as likely represent an extant undescribed species as an extinct progenitor of the species to which it is compared. According to Table 3, even closely related species, such as Amara alpina and A. bokeri, had apparently diverged from their common ancestor before late, early Pleistocene time. This seems to be true also for many species of the Cryobius complex. The only definite evidence of phyletic insect evolution at Cape Deceit is progressive wing reduction in Tachinus apterus, a very minor change considering the long period involved. Thus, fossil evidence presented here supports Coope's (1970) conclusion that evolution of insects has proceeded very slowly, much slower in fact than is thought by entomologists who have dealt with evolutionary and phylogenetic problems from the standpoint of relationships and distribution of the contemporary fauna (Ball, 1963; Ross, 1965; Barr, 1969). However, the evidence presented here pertains chiefly to Coleptera. Rates of evolution may well have been faster in other orders or in other regions (Downes, 1965).

The large number of extant Cryobius species in the oldest levels of the Cape Deceit sequence is surprising. Ball (1963) originally assumed that the subgenus achieved its present diversity largely through speciation in Pleistocene refugia, yet the duration of isolation in such

refugia would have been short compared to the longevity of some of the species listed in Table 3. Therefore, despite the close relationship of species in the Cryobius complex, diversification must have occurred earlier (Ball, 1969)--possibly early in the Pleistocene or during the late Pliocene when lowland tundra habitat was first forming in the Northern Hemisphere (Hopkins, et al., 1971). At that time the tundra environment would not have been continuous across the Holarctic area as it is at present. Different groups of tundra-adapted Cryobius species might have evolved in each of the disjunct tundra regions, yet all could have been derived from one or a few lineages of Cryobius known to have occurred in open areas of northern forests during the Pliocene (Hopkins, et al., 1971). Initial radiation of Cryobius in the new tundra environment probably happened quickly, but once most terricolous niches had been filled further speciation would have proceeded very slowly. Finally, when in middle Pleistocene time lowland tundra became continous across Holarctica, endemic species that had evolved earlier in the original disjunct tundra regions would have become widespread, resulting in the complex contemporary Cryobius fauna of many arctic regions. Though this explanation is largely a scenario, it is beginning to have a factual basis through current work on Pliocene and late Tertiary northern insect assemblages (Hopkins, et al., 1971). Moreover, it explains both the close relationship of Cryobius species and their apparent longevity. Other groups of closely related arctic insects may have had a similar evolutionary history. In other words, their taxonomic diversity, though not great, may be due to what occurred in the early Pleistocene or late Pliocene when the lowland tundra biome was first forming, rather than to climatic change and range disruptions of the late Pleistocene.

II. NON-PHYLETIC ECOSYSTEM EVOLUTION

Most ecosystem evolution at Deering has been primarily of the "non-phyletic" type--involving almost no *in situ* evolution of the members of the biotic portion of the system. Table 6 indicates environmental changes that occurred at Deering since initial deposition of the Cape Deceit Formation. For most of that time, the Deering areas was evidently the site of a functioning tundra ecosystem, but on at least three occasions treeline existed at or west of Deering. At the time of the last (Sangamon) interglacial it stood nearer to Deering than at present.

During Peat 1 interglacial, larches formed treeline in the Deering area. Why this should have been so in the early Pleistocene and not now is unclear, unless the fossils from Peat 1 represent *Larix dahurica* rather than the North American species *L. laricina*. Assuming they are of *L. laricina*, then the present restricted Alaskan distribution of that species (compared to its early Pleistocene distribution) may be an artifact of increasingly severe glacial climates causing progressive shrinking of *Larix* distribution during each cold phase.

Fossils show that the former tundra environment at Deering sometimes differed significantly from that of the present. The problem arises in determining whether such differences were of local or regional extent. Insects and plant fossils from Unit 2 of the Cape Deceit Formation indicate an environment quite different from that of the present, but some differences may be owing to local depositional conditions. For example, continuing deposition of silt would favor an abundance of *Artemisia* and hinder growth of mosses and dwarf birches (which often root in mosses) (Viereck, 1966), therefore partly explaining low *Betula* pollen percentages. On the other hand, low percentage of alder

pollen in Unit 2 spectra likely reflects regional conditions such as colder climate, but not necessarily an environment different from that which exists in contemporary Alaskan tundra areas where alders are absent.

Fossil data from Unit 2 of Deering Formation indicate both a local and regional environment that was more xeric and grassy than is the contemporary tundra. Frenzel (1968) refers to such an environment as steppe-tundra. Existence of steppe-tundra at Deering during late Wisconsin time agrees with evidence presented by Guthrie (1968), Yurtsev (1963; 1972), and Neilson (1968). But steppe-tundra there as late as 12,400 years ago contradicts Hopkins (IN PRESS 1972), who regards similarly aged evidence from Imuruk Lake and Kotzebue Sound (-38 m shore line samples) to be indicative of climatic warming of sufficient magnitude to create tundra dominated by dwarf-birch. Actually the two concepts are compatible, for dwarf birches did occur at Deering 12,400 years ago and furthermore, birch-dominated shrub tundra could have existed in certain areas of the Seward Peninsula while remnants of a formerly more extensive grassland-like environment existed elsewhere. Pollen data from Imuruk Zone K show a persistence of steppe-like conditions (high Artemisia and grass percentages) even after dwarf birches had become abundant there. That steppe-like conditions were not restricted to the Deering area in latest Wisconsin time is also indicated by presence of the grazing ungulates Bison, Mammuthus, and Equus in the vicinity of Imuruk at that time (Larsen, 1968; Colinvaux, 1964). Steppe conditions may have been more widespread on Seward Peninsula earlier in Wisconsin time; however, this part of the record is largely missing at Cape Deceit.

In spite of minor differences in the sequences at Cape Deceit and Imuruk, both indicate a trend toward grassy steppe-like tundra, culminating in late Pleistocene time. The explanation for this trend is obscure, but it ultimately implies regional aridity and possibly a more severe temperature regime during the late Pleistocene. A similar trend toward more severe late Pleistocene climates is documented in the mid-continent of the United States (Taylor, 1965) and Eurasia (Giterman and Golubeva, 1967; Frenzel, 1968; Grichuk, 1971). The last study (Grichuk, 1971) implies maximum extension of Eurasian cold steppe conditions toward Alaska in very latest Pleistocene time.

During the Pleistocene, steppe-tundra conditions existed throughout most of unglaciated Alaska (Guthrie, 1968; Matthews, 1970; unpublished manuscript, 1972), a fact with important implications for a variety of biological specialists. For example, the present tundra ecosystem in Alaska is being intensively studied under the auspices of the International Biological Program (IBP). A wealth of data has been accumulated and will be used to construct a mathematical model of the tundra ecosystem. Implicit in this approach is that only quantitative data may be used, and since the type of information discussed here and in other paleoenvironmental studies is not readily expressed numerically, it becomes very easy to assume that it is irrelevant to the study of tundra ecosystems. But these historical studies show that the tundra ecosystems have changed through time, and that the present tundra environment of unglaciated areas of Alaska is quite different from the environment of only 10,000 years ago. Surely, the structure and dynamics of the system have also undergone change during that time. Therefore, it seems appropriate that workers interested in the contemporary tundra ecosystem and its functioning take into account the growing body of knowledge

concerning its history. Indeed to do so would very quickly bring them into association with those working on grassland biome projects, for some of the contemporary features of the tundra system undoubtedly reflect its grassland or steppe history.

Compared to the Pleistocene fauna, the present Holarctic insect fauna is impoverished. With reference to vertebrates, this fact has been clear to paleontologists for a long time, but it has not been considered by entomologists who until recently were forced to work without the perspective offered by fossil evidence. Ross (1970), in his excellent paper on the origins of the prairie leafhopper fauna, acknowledges this problem when he states that "during the Pleistocene, patterns of prairie leafhopper evolution, dispersal, and extinction have been much more complex than the relatively simple patterns outlined ...". The occurrence of grassland conditions in large areas of Pleistocene Alaska and Siberia, a fact not likely to have been forseen by the study of the contemporary fauna alone, certainly confirms this statement.

Finally, some of the specific environmental evidence discussed here relates to a time when man is definitely known to have been in Alaska (Larsen, 1968; Mckennan and Cook, 1968), thereby giving archaeologists an insight as to the type of environment in which man lived and hunted. It should be obvious from this report that comparison of former man-occupied Alaskan environments with present day Alaskan treeless sites can be misleading.

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TABLE 1

SURFACE POLLEN SAMPLES[1]

Sample	Sample Type	Local Plant Community	Comments
74-67	Bottom mud at margin of a small pond	Sedge dominated pond margin. Pond in an area with "Cloud berry, dwarf shrub, marsh" type community (Hanson, 1953)	Sedge pollen probably over-represented.
73-67	Dry, turf plug	Dominant plants: Ledum, Arctostaphylos alpina. Plants present: Betula nana, Salix arctica, Carex spp., Vaccinium vitis-idea, Empetrum nigrum, Petasites sp., grasses.	Ericales and grass pollen probably over-represented. Artemisia growing within 100 m of sample site.
75-67	Bottom mud of a Carex marsh in a coastal gully	Sedges predominate. Sides of gully are grassy	Shrub birches are abundant at head of gully. Artemisia, Solidago, and other Compositae are abundant on vegetated parts of near-by coastal bluffs
105-69	Soil plug	Alder-willow-heath sere of a floodplain succession (Bliss and Cantlon, 1957). Dominant plants: Empetrum nigrum, Vaccinium uliginosum, Betula nana, willows, and Alnus crispa.	Ericales pollen probably over-represented Alnus pollen under represented.
97-69	Soil plug	Cloudberry-dwarf shrub-marsh community (Hanson, 1953). Empetrum nigrun and Rubus chamaemorus--co-dominants	Spruce pollen allochthonous. Rubus chamaemorus pollen under-represented

1. See Fig. 1 for location of sample sites.

TABLE 2

NORTHERNMOST TUNDRA ZONE (AFTER YOUNG, 1971) IN WHICH SELECTED CAPE DECEIT FOSSIL PLANT SPECIES ARE FOUND.

Taxon	Aquatic	Tundra Zone	Fossil Assemblage
Potamogeton alpinus	+	4[1]	S-2, S-11
P. gramineus[2]	+	4	S 13-67
P. praelongus[2]	+	4[3]	S-6
P. foliosus[2]	+	4[3]	S-5
P. filiformis	+	4	S-6
P. vaginatus	+	4[1]	S-6, S-11
Zanichellia palustris	+	4[1]	S-12
Hierochloe pauciflora		2	S-6
Trichophorum caespitosum		4[1]	S-6
Eleocharis uniglumis-palustris[7]	-+[4]	4[1]	S-6
Betula glandulosa-nana[7]		4-3[5]	S-6, S-11
Alnus sp.[6]		4	see pollen diag.
Polygonum sect. persicaria[6]	+[5]	4[3]	see pollen diag.
Ranunculus trichophyllus	+	3	S-6, 58-69
R. sceleratus		4[1], 3	S-6, S 13-67, S-11
Thalictrum alpinum		3[1]	52-67, 27-67
Lepidium densiflorum		4[1], 3	S-6
Barbarea orthoceras		4[1], 3	S-6, 55-67, 31-67, 33-67, S 13-67
Arabis lyrata		4[1]	81-69
Myriophyllum spicatum	+	4	S-6
Empetrum nigrum		3	S-5, S-1, 54-67, S-2
Menyanthes trifoliata	+[4]	4	S-6, S-1, S-12, S 13-67, S-11

1. Northern limit determined using Hultén (1968).

2. Specific determination questioned in Fig. 12.

3. Hardly or not a tundra plant at present in Alaska (Hultén, 1968).

TABLE 2 (Cont.)

4. Emergent aquatic

5. Depending on which species is represented

6. Represented by pollen only

7. Either or both named species represented.

TABLE 3

INVERTEBRATE FOSSILS FROM THE CAPE DECEIT SEQUENCE

		Samples (see Fig. 7)											
	ECOL.[1]	S-11	D-1	Peat 1	S10-67	S13-67	S-14	S-12	Peat 4	S-1	S-7	Peat 5	S-5	S-6
INSECTA														
Heteroptera														
Corixidae														
Callicorixa sp.	a	—	—	—	—	—	—	—	—	—	—	—	—	2?
Lygaeidae, Genus? sp.		—	—	—	—	—	—	—	—	—	—	—	—	1[2]
Saldidae														
Chiloxanthus stellatus (Curtis)	Ab1-2	—	—	—	—	+[3]	—	—	—	—	—	—	1	1
Calacanthia sp.		—	—	—	—	—	—	—	—	—	—	—	—	1?
Teloleuca sp.		—	—	—	7?	—	—	—	—	—	—	—	—	—
Salda littoralis (L.)	Bc1-2	—	—	—	—	—	—	—	—	—	—	—	—	10[2]
Homoptera														
Cicadellidae														
Athysanella spp.	D	—	—	—	—	—	—	—	—	—	—	—	—	22
Deltocephalus cf balli Van Duzee	D?	—	—	—	—	—	—	—	—	—	—	—	—	3
D. cf pulicaris (Fall)	D?	—	—	—	—	—	—	58[2]	—	149	—	—	—	—
Deltocephalus sp.		—	—	—	—	—	—	—	—	—	—	—	4	21
Genus? sp.		—	—	+	—	—	—	—	—	—	—	—	—	—
Caliscelidae														
Aphelonema sp.	D	—	—	—	—	—	—	—	—	—	—	—	—	1
Psyllidae														
Trioza quadripunctata Crawford		—	—	—	—	—	—	—	—	—	—	—	—	2
Trioza sp.		—	—	—	—	—	—	—	—	—	—	—	—	1
Coleoptera														
Carabidae														
Carabus truncaticollis Eschz.	Ac3	—	+	+	2	+	—	—	—	—	—	—	1	4
Pelophila borealis Payk.	Bb2	—	—	+	—	—	—	—	—	—	—	—	—	—
Notiophilus semistriatus Say	'B'd2	—	—	—	1?	—	—	—	—	—	—	—	—	—
N. borealis Harris	Bd2	—	—	—	—	—	—	—	—	—	—	—	2?	—
Notiophilus sp.		—	—	—	—	—	—	—	—	—	—	—	—	1
Diacheila polita Fald.	"B"c3	—	—	+	2	—	—	—	—	—	—	—	1	2
Elaphrus lapponicus Gyll.	'B'b2	—	—	*+a[3]	—	—	—	—	—	—	—	—	—	—
Elaphrus sp.		—	—	—	—	+	—	—	—	—	—	—	—	—
Dyschirius frigidus Mann.	'B'c2	—	—	—	1	—	—	—	—	—	—	—	1	—
D. nigricornis Motsch.	Bc2	—	—	+	—	—	—	—	—	—	—	—	—	—
Dyschirius sp.		—	—	—	—	—	—	—	+	—	—	—	—	—
Patrobus sp.		—	—	—	—	—	—	—	+	—	—	—	—	—
Bembidion (Plataphodes) sp.		—	—	—	1	—	—	—	—	—	—	—	—	—
B. (Peryphanes) sp.		—	—	+	—	—	—	—	—	—	—	—	—	—
B. umiatense Lth.		—	—	*+a?	—	—	—	—	—	—	—	—	—	—
Bembidion sp.		—	—	—	—	—	—	1	—	—	—	—	—	—
Pterostichus nearcticus Lth.	Ad1	—	—	—	—	—	—	—	—	—	—	—	—	1
P. (Cryobius) soperi Ball	Ad2	—	—	—	—	—	—	—	—	—	—	—	—	*25
P. (Cryobius) kotzebuei Ball	A	—	—	—	1	—	—	1?	—	—	—	—	—	1
P. (Cryobius) tareumiut Ball	Ac3	+	—	*+a	—	+	—	—	—	1	—	—	7	—

TABLE 3 (Cont.)

		Samples (see Fig. 7)												
	ECOL.[1]	S-11	D-1	Peat 1	S10-67	S13-67	S-14	S-12	Peat 4	S-1	S-7	Peat 5	S-5	S-6
P. (Cryobius) hudsonicus Lec.	'B'c2	—	—	—	—	—	—	—	+a	—	—	—	—	—
P. (Cryobius) similis Mann.	Bc2	++	+	+	8	*++	—	—	—	—	—	—	3	1?
P. (Cryobius) parasimilis Ball	Ac3	—	—	—	—	—	—	—	*+a	—	—	+a	*31	—
P. (Cryobius) similis sp. grp.		—	—	—	—	—	—	—	—	—	—	—	7	—
P. (Cryobius) tiliaceoradix Ball	Bc1	—	—	—	*4	+	—	—	—	—	—	—	—	—
P. (Cryobius) biocryus Ball	A	—	—	—	*1	—	—	—	—	—	—	—	—	—
P. (Cryobius) pinguedineus Eschz.	Bc3	—	—	—	*16	+	—	1	+a	—	—	—	*22	*18
P. (Cryobius) auriga Ball	A	—	+	—	—	—	—	*5	—	1	*+	—	—	—
P. (Cryobius) ventricosus Eschz.	Bc2	—	+	+?	*4	—	—	—	—	4	—	++a	*41	1
P. (Cryobius) brevicornis Kby.	Bc2	—	+	—	4	—	—	—	+a	1	—	—	5	3
P. (Cryobius) mandibularoides Ball	A	—	—	—	*9	—	—	—	—	—	—	—	—	—
P. (Cryobius) nivalis Sahlb.	Ac3	—	—	+a	4	—	—	—	—	*2	—	—	*83	*29
P. (Cryobius) cf nivalis Sahlb.		—	—	*+a	—	—	—	—	—	—	—	—	—	—
P. (Cryobius) brevicornis sp. grp.		+	—	—	—	—	—	—	—	—	—	—	5	—
P. (Cryobius) sp.		+	—	+	18	+	—	2	—	4	—	—	16	35
P. vermiculosus Men.	Ac	+a	—	+	—	—	—	—	—	1	—	—	—	—
P. agonus Horn	Ac3	—	—	—	—	—	—	—	—	—	—	+a	7	—
P. costatus Men.	Ab3	—	+	+a	—	—	—	—	—	—	—	—	—	1
P. sublaevis Sahlb.	Ad2	—	—	—	—	—	—	—	—	—	—	—	—	4
P. haematopus Dej.	Bc2	—	—	—	3	—	—	—	—	1	—	*+a	3	11
Agonum exaratum Mann.	Bb3	—	—	+	—	—	—	—	—	—	—	—	—	—
Agonum sp.		—	—	—	—	—	—	—	+	—	—	—	—	—
Amara alpina Payk.	Ad2	—	—	—	37	+	—	*107	—	37	+	+a?	21	*154
A. bokeri Csiki	A	—	+?	—	11	+	—	—	—	—	—	—	—	3
A. hyperborea Dej.	Bc1	+?	—	—	—	—	—	—	—	—	—	—	—	—
A. (Curtonotus) sp.		—	—	+	—	—	—	—	—	—	—	—	—	—
A. browni Lth.	Bc	—	—	—	—	—	—	—	—	—	—	—	—	1?
A. (Celia) sp.		—	—	—	—	—	—	—	—	—	—	—	—	2
Harpalus amputatus Say	DCd	—	—	—	—	—	—	—	—	—	—	—	—	5
H. nigritarsis Sahlb.	Bd2	—	—	—	—	—	—	—	—	—	—	—	—	1
H. cf alaskensis Lth.		—	—	—	—	—	—	—	—	—	—	—	—	a
Trichocellus mannerheimi Sahlb.	Ad2	—	—	—	—	—	—	—	—	—	—	—	—	16
Dytiscidae														
Hydroporus sp.	d	—	—	+	—	—	—	—	—	—	—	—	—	1
Agabus sp.	a	—	—	+?	—	—	—	—	—	—	—	—	—	2
Ilybius sp.	a	—	—	+?	—	—	+	—	—	—	—	—	—	—
Neoscutopterus cf horni Lec.	Ba	—	—	+	—	—	+a	—	—	—	—	—	—	—
Colymbetes sp.	a	—	—	—	—	—	—	+	—	—	—	—	—	—
Hydrophilidae														
Helophorus splendidus Sahlb.	Aa	—	—	+	—	—	—	—	—	—	—	—	—	3
Helophorus sp.	a?	—	—	+	1	+	—	—	—	—	—	—	—	—
Cercyon sp.		—	—	—	—	—	—	—	—	—	—	—	—	1
Staphylinidae														
Megarthrus sinuaticollis Boisd.	B	+	—	—	—	—	—	—	—	—	—	—	—	—
Arpedium brachypterum (Grav.)	Bc3	—	—	—	—	—	—	—	—	1	—	—	—	—
Olophrum sp.		—	+	—	1	—	—	—	+	—	—	—	—	—
Boreaphilus henninglanus Sahlb.		—	—	—	—	—	—	—	—	—	—	—	—	1
Subhaida sp (undescribed sp.)		—	—	—	1	—	—	—	—	42	—	—	—	1
Micralymma brevilingue Schiødt.	Ac	—	—	+	66	+	—	35	—	89	—	—	—	33

TABLE 3 (Cont.)

	ECOL.[1]	Samples (see Fig. 7) S-11	D-1	Peat 1	S10-67	S13-67	S-14	S-12	Peat 4	S-1	S-7	Peat 5	S-5	S-6
Stenus spp.	b	—	—	++	6	+	—	2	+	3	—	—	2	1
Lathrobium sp.		—	—	—	—	—	—	—	—	—	—	—	1	8
Quedius spp.		—	—	++	2	—	—	—	+	—	—	—	—	1
Tachinus apterus Makl.	A	—	—	—	*310	*++	—	*12	—	*16	—	—	*63	*147
T. nearcticus Campbell	B	—	—	—	—	—	—	—	—	—	—	—	—	1
Tachinus sp.		—	—	+	—	—	—	—	—	1	—	—	—	—
Tachyporus sp.		—	—	+	—	—	—	—	—	—	—	—	—	2
Bolitobius sp.		—	—	—	—	—	—	1?	—	—	—	—	—	—
Gymnusa brevicollis Payk.	Bb3	—	—	+	—	—	—	—	—	—	—	—	—	—
Aleocharinae, Genus? sp.		—	—	—	8	—	—	3	—	—	—	—	—	65
Leptodiridae														
Colon sp.		—	—	—	2	—	—	—	—	—	—	—	—	2
Scydmaenidae, Genus? sp.		—	—	—	—	—	—	—	+	—	—	—	—	—
Scarabaeidae														
Aphodius cf distinctus (Mull.)		—	—	—	—	—	—	—	—	—	—	—	—	69
Byrrhidae														
Simplocaria basalis Sahlb.		—	—	—	—	—	—	—	—	1?	—	—	—	—
S. elongata Sahlb.		—	—	+	—	—	—	—	—	—	—	—	—	—
Morychus aeneolus (Lec.)	A	—	—	—	—	—	—	—	—	—	—	—	—	236?
Byrrhus sp.		+	—	—	1	+	—	1	—	—	—	—	—	—
Curimopsis setulosa (Mann.)		—	—	—	—	—	—	—	—	—	—	—	—	6?
Elateridae														
Denticollis varians (Germ.)	Bd	—	—	—	—	—	—	—	—	—	—	—	—	1
Coccinellidae														
Scymnus sp.		—	—	—	—	—	—	—	—	—	—	—	—	1
Ceratomegilla sp.		—	—	—	—	—	—	—	—	—	—	—	—	1
Genus? sp.		—	—	—	—	—	—	—	—	—	—	—	1	4
Lathridiidae														
Enicmus sp.		—	—	—	—	—	—	—	+	—	—	—	—	—
Genus? sp.		—	—	+	—	—	—	—	—	—	—	—	1	2
Chrysomelidae														
Donacia sp.	a	—	—	—	—	—	—	1	—	—	—	—	—	—
Chrysolina subsulcata (Mann.)	A	—	—	—	—	—	—	—	—	*11	—	—	—	*2
C. subsulcata sp. grp.		—	—	+a	5	—	—	—	—	6	—	—	6	10
C. cavigera (Sahlb.)	A	—	—	—	—	+cf	—	—	—	—	—	—	—	1?
C. caurina Brown	A	—	—	—	—	—	—	—	—	—	—	—	—	5
C. flavomarginata vidua (Rogers)	D	—	—	—	—	—	—	—	—	—	—	—	1?	—
C. hudsonica Brown	B	—	—	—	—	—	—	—	—	6?	—	—	—	1?
C. cf rufilabris (Fald.) sp. B		—	—	—	—	—	—	—	—	—	—	—	—	*1
C. cf rufilabris (Fald.) sp. C		—	—	—	—	—	—	—	—	*11	—	—	—	—
C. basilaris (Say)	B?	—	—	—	2?	—	—	—	—	—	—	—	—	9
Chrysolina sp. A		—	—	—	—	—	—	—	—	—	—	—	—	22
Chrysolina spp.		—	—	—	—	—	—	—	—	—	—	—	—	7
Chrysomela sp.		—	—	—	1	—	—	—	—	—	—	—	—	—
Phaedon cf cyanescens Stål		—	—	—	2	+	—	—	—	—	—	—	—	—
Phaedon sp.		—	—	—	—	—	—	—	—	—	—	—	—	5
Hydrothassa cf vittata Oliver	a	—	—	—	—	—	—	—	—	—	—	—	—	2
Alticinae, Genus? sp.		—	—	—	—	—	—	—	+	—	—	—	—	—
Cassida flavcola Thunb.	B	—	—	+	—	—	—	—	—	—	—	—	—	—

TABLE 3 (Cont.)

		Samples (see Fig. 7)											
	Ecol.[1]	S-11	D-1	Peat 1	S10-67	S13-67	S-14	S-12	Peat 4	S-1	S-7	Peat 5	S-5	S-6
Curculionidae														
Hypera seriatus (Mann.)	A	—	—	—	—	—	—	—	—	—	—	—	—	5
Hypera sp.		—	—	+?	—	—	—	—	—	—	—	—	3	1
Lepidophorus lineaticollis Kby.	Bd2	—	—	—	—	—	—	5	—	4	—	—	38	597
Vitavitus thulius Kissinger		—	—	—	91	++	—	—	—	—	—	—	—	—
Lepyrus gemellus Kby.	B	—	—	—	—	—	—	—	—	—	—	—	—	1
L. canadensis Csy.	B	—	—	—	—	—	—	—	—	—	—	—	—	1?
L. stefanssoni (Leng)	B	—	—	—	—	—	—	—	—	—	—	—	4	1
L. cf labradorensis Blair		—	—	—	2	—	—	—	—	—	—	—	1	1
L. cf palustris Scop.		—	—	—	—	—	—	—	—	—	—	—	2	—
Lepyrus sp.		—	—	—	—	—	—	—	—	—	—	—	—	1
Cleonus plumbeus (Lec.)	B	—	+?	—	1	+	—	—	—	1	—	—	—	7
Dorytomus sp.		—	—	—	—	—	—	—	—	—	—	—	2	—
Notaris aethiops Fab.	B?	—	—	—	—	—	—	1?	—	—	—	—	—	—
N. cf flavipilosus Chitt.		***a	—	—	5	—	—	—	—	—	—	—	—	—
Apion sp.		—	—	—	5	—	—	1	—	—	—	—	1	—
A. (Eutrichapion) cyanitictum Fall	B	—	—	—	—	—	—	—	—	—	—	—	—	20?
A. (Eutrichapion) sp.		—	—	—	—	+	—	—	—	—	—	—	1	—
Rhynchaenus sp.		—	—	+?	4	—	—	—	—	—	—	—	2	35
Ceutorhynchus sp.		—	—	—	70	++	—	—	—	—	—	—	—	2
C. cf subpubescens Lec.		—	—	—	8	+	—	—	—	—	—	—	—	—
Lepidoptera, larval fragments		—	—	—	++	+	—	++	—	++	+	—	—	+
Diptera														
Tipulidae														
Tipula (Vestiplex) bergrothiana Alex.		—	—	—	—	—	—	—	—	—	—	—	1?	4?
Tipula (Vestiplex) sp.		—	—	+	15	+	—	—	—	—	—	—	1	4
Bibionidae, Genus? sp.		—	—	—	—	—	—	—	—	—	—	—	—	1
Xylophagidae														
Xylophagus abdominalis Loew	B	—	—	—	1	+?	—	2?	—	—	—	—	—	1
Milichiidae														
Meoneura sp.		—	—	—	—	—	—	1	—	—	—	—	—	—
Calliphoridae, Genus? sp.		—	—	—	—	—	—	3	—	—	—	—	—	—
Hymenoptera														
Symphyta														
Tenthredinidae														
Nematus sp.		—	—	—	1	+	—	—	—	13	—	—	—	4
Apocrita					56[4]			4[4]		76[4]			4[4]	47[4]
Braconidae														
Meteorus sp.		—	—	—	+?	—	—	—	—	—	—	—	—	2
M. leviventris Wesm.		—	—	—	—	—	—	—	—	—	—	—	—	5
Macrocentrus sp.		—	—	—	—	—	—	—	—	13	—	—	—	1
Orgilus sp.		—	—	—	—	—	—	—	—	—	—	—	—	7
Diospilus sp.		—	—	—	—	—	—	—	—	—	—	—	—	1?
Agathis sp.		—	—	—	—	—	—	—	—	—	—	—	—	2
Agathidinae, Genus? sp.		—	—	—	+?	—	—	—	—	—	—	—	—	—
Ichneutes sp.		—	—	—	+	—	—	—	—	—	—	—	—	2
Chelonus spp.		—	—	—	+	—	—	—	—	—	—	—	—	2
C. (Microchelonus) sp.		—	—	—	+	—	—	—	—	—	—	—	—	—
Alysiinae, Genus? sp.		—	—	—	—	—	—	—	—	+	—	—	—	—

TABLE 3 (Cont.)

	ECOL.[1]	Samples (see Fig.7) S-11	D-1	Peat 1	S10-67	S13-67	S-14	S-12	Peat 4	S-1	S-7	Peat 5	S-5	S-6
Rogas sp.		—	—	—	+	+	—	—	—	—	—	—	—	3
Ichneumonidae														
Bathythrix sp.		—	—	—	+	—	—	—	—	—	—	—	—	1
Aclastus sp.		—	—	—	—	—	—	—	—	—	—	—	—	1
Endasys sp.		—	—	—	—	—	—	—	—	—	—	—	—	2
Phygadeuon sp.		—	—	—	+	—	—	—	—	—	—	—	—	—
Atractodes sp.		—	—	—	+	—	—	—	—	—	—	—	—	2
Oresbius spp.		—	—	—	—	—	—	—	—	+	—	—	—	5
Buathra laborator fabricii (Schiødt.)		—	—	—	—	—	—	—	—	—	—	—	—	1
Phacogenes sp.		—	—	—	—	—	—	—	—	—	—	—	—	4
Ichneumon sp.		—	—	—	+	—	—	—	—	—	—	—	—	4
Coelichneumonops sp.		—	—	—	—	—	—	—	—	—	—	—	—	1
Glypta ap.		—	—	—	—	—	—	—	—	—	—	—	—	1
Ctenopelmatinae, Pionini		—	—	—	—	—	—	—	—	—	—	—	—	1?
Proclitus sp.		—	—	—	—	—	—	—	—	—	—	—	—	6
Plectiscinae, Genus? sp.		—	—	—	—	—	—	+	—	—	—	—	—	—
Stenomacrus sp.		—	—	—	—	—	—	—	—	—	—	—	—	1
Hyposoter sp.		—	—	—	+?	—	—	—	—	—	—	—	—	1?
Cremastinae, Genus? sp.		—	—	—	+	—	—	—	—	—	—	—	—	2
Anomalon sp.	D	—	—	—	—	—	—	—	—	—	—	—	—	4
Anomalinae, Genus? sp.		—	—	—	+	—	—	—	—	—	—	—	—	—
Mesochorus sp.		—	—	—	+	—	—	—	—	+	—	—	—	2
Pteromalidae														
Pteromalini, Genus? sp.		—	—	—	+	—	—	—	—	—	—	—	—	—
Eurytomidae														
Eurytoma cf gigantea Walsh		—	—	—	—	+	—	—	—	—	—	—	—	—
Gasteruptiidae														
Gasteruption sp.		—	—	—	—	—	—	—	—	—	—	—	—	1
Proctotrupidae														
Codrus sp.		—	—	—	—	—	—	—	—	—	—	—	—	1
Diapriidae														
Atelopsilus or Synacra sp.		—	—	—	—	—	—	—	—	—	—	—	—	1
Formicidae														
Leptothorax canadensis Prov.	'B'd	—	—	—	—	—	—	—	++	—	—	—	—	—
Camponotus herculeanus (L.)	C	—	—	—	—	—	—	—	+	—	—	—	—	—
Apidae														
Pyrobombus sp. (worker)		—	—	—	+	—	—	—	—	—	—	—	—	—
ARACHNIDA														
Acari														
Oribatidae														
Ameronothrus sp.		—	—	—	—	—	—	—	+	—	—	—	—	—
Araneae														
Lycosidae														
Trochosa sp.		—	—	—	—	—	—	—	—	—	—	—	—	3
Tarentula pictilis (Emerton)		—	—	—	—	—	—	—	—	—	—	—	1	—
Lynyphiidae														
Erigone sp	b	—	—	—	+	—	—	—	—	—	—	—	—	10
Eperigone sp.		—	—	—	—	—	—	—	—	—	—	—	—	1?

TABLE 3 (Cont.)

		Samples (see Fig. 7)											
	ECOL.[1]	S-11	D-1	Peat 1	S10-67	S13-67	S-14	S-12	Peat 4	S-1	S-7	Peat 5	S-5	S-6
CRUSTACEA														
Notostraca														
Lepidurus sp.	a	—	—	—	+	—	—	+	—	+	—	—	—	+
Cladocera														
Daphnia (*Daphnia*) sp.	a	—	—	—	+	—	—	—	+	—	—	—	—	+
D. (*Ctenodaphnia*) sp.	a	—	—	—	—	—	—	—	—	—	—	—	—	+
BRYOZOA														
Cristatella sp.	a	—	—	—	+	—	—	+	—	+	—	—	—	+

FOOTNOTES

1. ECOL. -- habitat requirements:

   Regional: A = Obligate tundra
   B = Tundra and forest
   'B' = Scarcely beyond treeline
   "B" = Open sites when found below treeline
   C = Obligate forest
   D = Grassland

   Local: a = aquatic
   b = hygrophilous
   c = damp to mesic sites
   d = xeric sites

   Vegetation: 1 = scantily vegetated (e.g., bare floodplain areas)
   2 = moderately vegetated
   3 = complete vegetation cover (e.g., continuous turf)

2. Number refers to minimum number of individual insects

3. Symbols: cf = Species near but probably not the named species (possibly undescribed)
   ? = Fossils lack diagnostic characters needed for positive determination, or suitable series of reference specimens not available.
   + = Taxon present; ++ = Taxon abundant
   a = Some fossils partially articulated
   * = Some fossils include diagnostic genitalia

4. Hymenoptera, Apocrita: Fossils are still under study. Number refers to total individuals of Apocrita (mostly Ichneumonoidea) in each sample.

TABLE 4

MINIMUM NUMBER OF ARTHROPOD INDIVIDUALS

IN EACH QUANTITATIVELY ANALYZED ASSEMBLAGE

Assemblage	Minimum Number of Individuals[1]	Amount of Sediment processed (Kg)
S 10-67 (Cape Deceit Fm.)	806	340
S-12 (Inmachuk Fm.)	246	520
S-1 (Deering Fm., Unit 1)	509	283
S-5 (Deering Fm., Unit 2)	398	227
S-6 (Deering Fm., Unit 2)	1655	220

1. See Matthews (1968) for method of computation.

TABLE 5

REVISION OF EVA CREEK FOSSIL ARTHROPOD LIST

(LATE PLEISTOCENE, INTERIOR ALASKA)[1].

As Originally Listed:[1].	Change to or Add:
Carabidae	
Cymindis sp.	*Cymindis unicolor* Kirby or a closely related undescribed species.
Genus sp.	*Harpalus amputatus* Say
_____	*Hydrobius fuscipes* Leach (Hydrophilidae). Sample 3-1A.
Omaliinae	
Olophrum sp.	*Olophrum latum* Makl.
Micralymma sp.	*Micralymma brevilingue* Schiødt.
Tachyporinae	
Tachinus sp. A	*Tachinus apterus* Makl.
Tachinus sp. B	*Tachyporus* sp.
Scarabaeidae	
Aphodius sp. B	[2]*Aphodius* of *pectorialis* or *duplex*
Byrrhidae	
Curimopsis sp.	*Curimopsis setulosa* Mann. ?
Caenocara sp.	move to Anobiidae
Morychus sp. A, sp. B	Represent one species only.
Elateridae	
Genus sp. A	*Denticollis varians* (Germ.)[3]
Genus sp. B	*Negastrius extricatus* (Fall)?[3]
Curculionidae	
Genus spp.	most fossils are *Lepidophorus lineaticollis* Kirby. Also present: *Sitona* sp.--sample 3-1A: *Hypera* of *castor* (Lec.) sample 3-3C.

TABLE 5 (Cont.)

As Originally Listed:	Change to or Add:
Family and Genus Unknown	
Genus sp. A	*Pissodes* sp. (Circulionidae)
Genus sp. B	*Apion* sp. (Curculionidae)
Genus sp. C	*Rhynchaenus* sp. (Curculionidae)
Genus sp. D	*Dorytomus* cf *alaskanus* Csy. (Curculionidae)
Genus sp. F	Lathridiidae
Genus sp. I	*Laccobius* ? sp. (Hydrophilidae)
Genus sp. J	Lathridiidae
Genus sp. N	*Ceutorhynchus* sp. (Curculionidae)
Genus sp. Q	*Colon* sp. (Leptodiridae)
_____	*Xylophagus* sp. (Diptera), samples 3-3B, 3-3C
_____	*Tipula* (Vestiplex) sp. (Diptera) sample 3-3C
_____	Cicadellidae (Homoptera) sample 3-3C

1. Matthews, 1968 for original list and sample designations
2. Ident. by: H.F. Howden, Carleton Univ.
3. Ident. by: E.C. Becker, CNC, Ottawa

TABLE 6

SUMMARY OF QUATERNARY ENVIRONMENTAL HISTORY AT DEERING, ALASKA

TIME	STRATIGRAPHIC UNIT	PALEOENVIRONMENT
Late Holocene	Unit 2, Deering Formation, Sample 72-67	TUNDRA: Similar to present at Deering. Dwarf birches wide spread; alders in the valleys and at other protected sites. Formation of thick moss-peat and turf in the Cape Deceit-Deering area. CLIMATE: Like that of the present.
Early Holocene, circa 9000 yrs. BP	Unit 2, Deering Formation, and Peat 6	TUNDRA: Dwarf birches abundant, but alders possibly more rare than at present. Larix possibly present in Deering area, but other conifers no closer than at present. Silt deposition at Cape Deceit ceases around 9000 BP; followed by peat formation (in some areas) and another phase of silt deposition preceding formation of late Holocene moss-peat. CLIMATE: Colder than at present if low percentage of alder pollen in Peat 6 represents regional conditions.
Late Wisconsin, (Late Weichsel)[1], circa 12400 yrs. BP	Unit 2 (upper part), Deering Formation	STEPPE-TUNDRA: Poa, Artemisia, and Potentilla locally abundant. Prairie insects, not present today in Alaska, occur at Deering. Grazing ungulates (e.g., Bison, Equus) present in the Seward Peninsula region. Grassy environment at Deering may be remnant of a formerly more extensive steppe-like environment. Small seasonal ponds exist at Cape Deceit. CLIMATE: Colder than at present, but not so cold as to prohibit growth of dwarf birches. Tundra Zone 3 or 4 according to Young's zonation scheme (1971).
Early Wisconsin?, (Early Weichsel?)	Basal Unit 2, Deering Formation, at Station 1	TUNDRA: Possibly steppe-like, certainly locally grassy. Dwarf birches and alders very rare. Crucifers abundant in local environment. CLIMATE: Too cold for growth of dwarf birches and alders? Certainly colder than at present. Probably colder than during latest Wisconsin, but not as arid as at that time.
Sangamon = Pelukian Interglacial (Eemian)	Peat 5 and basal Unit 2, Deering Formation, at Station 8	TUNDRA: Shrubby; dwarf birches and alders present. Alders probably growing in interfluve areas, unlike the present situation. Spruce treeline closer to Deering than at present Silt depositon ceases; peat forms in some areas ; and following this organic silts are deposited and disturbed by solifluction. Shoreline of Pelukian embayment (which inundated lower Inmachuk valley) exists near Cape Deceit Station 8. CLIMATE: Warmer than at present, but not warm enough at Deering for survival of spruce.
Illinoian (Saal)	Upper Unit 1, Deering Formation	TUNDRA: Herbaceous-- dwarf birches and alders very rare. Spruce treeline much more distant from Deering than at present. Fell-field environment prevails locally. Dessication cracks form at Cape Deceit. Loess deposition increases during deposition of the upper part of the unit. CLIMATE: Colder than at present and locally arid. Regional climate perhaps not as arid as during late Wisconsin. Temperature regime possibly like that of contemporary Barrow, Alaska (Tundra Zone 3 -- Young, 1971).
Illinoian (Saal)	Unit 1, henseli Zone, Deering Formation	TUNDRA: Alders more rare than at present, but dwarf birches probably exist at Deering. Local environment probably with more continuous vegetation cover than during deposition of overlying silts. Potentilla and crucifers locally abundant. CLIMATE: Probably colder than present at Deering, but not as cold as during deposition of overlying Unit 1 silts. Local environment arid. Regional environment possibly arid, but not to the degree seen in late Wisconsin time.
Early Illinoian (Saal)	Deering Formation sediments immediately above Peat 4 at Station 8 (Fig. 6C).	TUNDRA: Birches (probably dwarf or shrub) present in Deering region. Alders present near Cape Deceit during part of time interval, but at other times apparently not occurring there. A few apomictic spruce survive in Deering area. Polyploid species of grass occur at Cape Deceit during phase of congeliturbation and sand deposition immediately following preceding interglaciation. CLIMATE: As at present in Deering area or slightly colder?
Kotzebuan (Holstein?) Interglacial	Peat 4, Stations 8 and 9	FOREST: Or forest-tundra. White spruce, black spruce, and arboreal birch present at Deering. Forest insects occur at Deering along with some tundra species. If treeline not at Deering, then not far west of Deering. CLIMATE: As warm as present day interior Alaska, but probably not as continental due to proximity of Kotzebuan sea (Hopkins,1967b).

TABLE 6 (Cont.)

TIME	STRATIGRAPHIC UNIT	PALEOENVIRONMENT
Pre-Kotzebuan glaciation	Organic silts immediately below Peat 4, Station 8	TUNDRA: Alders and birches rare? CLIMATE: Probably colder than at present
Middle Pleistocene interglacial ?	Represented by hiatus between Inmachuk and Deering formations at some parts of the exposure.	_____: Erosional interval
("Cromerian"[2]) glacial	Inmachuk Formation, including Peat 3	TUNDRA: Early -- during deposition of sands at Cape Deceit, willows abundant, and Artemisia more abundant than at present. Later--during period of silt deposition at Cape Deceit, dwarf birches and Sphagnum more abundant. Potentilla locally abundant during silt deposition. Alders rare in Cape Deceit area during all of Inmachuk time. Slowing silt deposition in late Inmachuk time results in formation of silty to felted peat. Willows locally abundant. Small ponds exist in some areas during Peat 3 time. During and following peat formation, an episode of solifluction (?) mobilizes Peat 3 and the underlying few meters of sediment. CLIMATE: During deposition of silts and sands, colder than at present; but apparently not too cold for growth of dwarf birches. During formation of Peat 3 and congeliturbation episode, local environment damp and regional climate possibly as at present.
("Cromerian") interglacial	Represented by hiatus between Inmachuk and Cape Deceit formations	FOREST?: Larix possibly in Deering area (note Larix wood at contact of Inmachuk and Cape Deceit formations, Fig. 7). Otherwise, local and regional flora unknown. Period of thawing, erosion, and slumping CLIMATE: As warm or warmer than at present in Deering region. Most probably like present climate of interior Alaska, though not as continental.
("Cromerian") glacial	Unit 2 and Peat 2, Cape Deceit Formation	TUNDRA: Alders rare, dwarf birches probably not as abundant as now. Potentilla locally abundant. Sedge peat forms during phase of reduced silt deposition late in Cape Deceit time. Possibility of solifluction episode during and after formation of Peat 2, but preceding erosional interval mentioned above. During deposition of organic silts, Artemisia more abundant locally (and possibly regionally) than at present. CLIMATE: Colder than at present, possibly more arid regionally. Permafrost exists in the Deering area.
("Cromerian") interglacial	Peat 1, Cape Deceit Formation	FOREST-TUNDRA: Scattered groves of larches, but no spruces, exist at Deering. Following peat formation, renewed silt deposition and/or colder climate results in death of trees and they are rebedded to form woody zones immediately above Peat 1. Fens with well developed submerged and emergent vegetation exist at Cape Deceit during Peat 1 time. CLIMATE: Warmer than at present in the Deering area, but probably not as warm as interior Alaska today.
("Cromerian") glacial or interglacial	Unit 1, Cape Deceit Formation	TUNDRA: Regionally dwarf birches and alders as abundant as at present. Sedges and/or Potentilla locally abundant at times. Sedge peats form during an early depositional phase. Solifluction occurs during early depositional phase. CLIMATE: Like that of the present.
("Cromerian") interglacial	Unit 1, Cape Deceit Formation, Sample 79-68 (Fig. 7)	FOREST: Spruces growing at Deering or in the immediate vicinity. Alder and Botrychium locally abundant. CLIMATE: Warmer than at present. Similar to present day interior Alaska.
Glacial?	"Kittik" (Fig. 3)(Guthrie and Matthews, 1971)	_____: Periglacial environment in which mechanical weathering of metalimestone occurs. CLIMATE: Periglacial

FOOTNOTES:

1. North European stages listed in parentheses
2. "Cromerian" used as in Zagwijn, et al., 1971.

Fig. 1 Location of Cape Deceit, Deering, and the fossil locality. Numbers refer to collection sites of surface pollen samples (Fig. 10, Table 1). Surface sample 97-69 located at "Pingo" (Fig. 2).

CAPE DECEIT
73-67
74-67
75-67
fossil locality
station 8
DEERING
Inmachuk R.
105-69
Barrow
CHUKCHI SEA
Cape Thompson
Umiat
BROOKS RANGE
SEWARD PEN.
Deering
Nome
Fairbanks
RANGE
ALASKA
GULF OF ALASKA

Figure 1

Fig. 2 Seward Peninsula region: showing localities mentioned in the text, extent of late Pleistocene glaciers, present position of treeline, and location of a former shoreline.

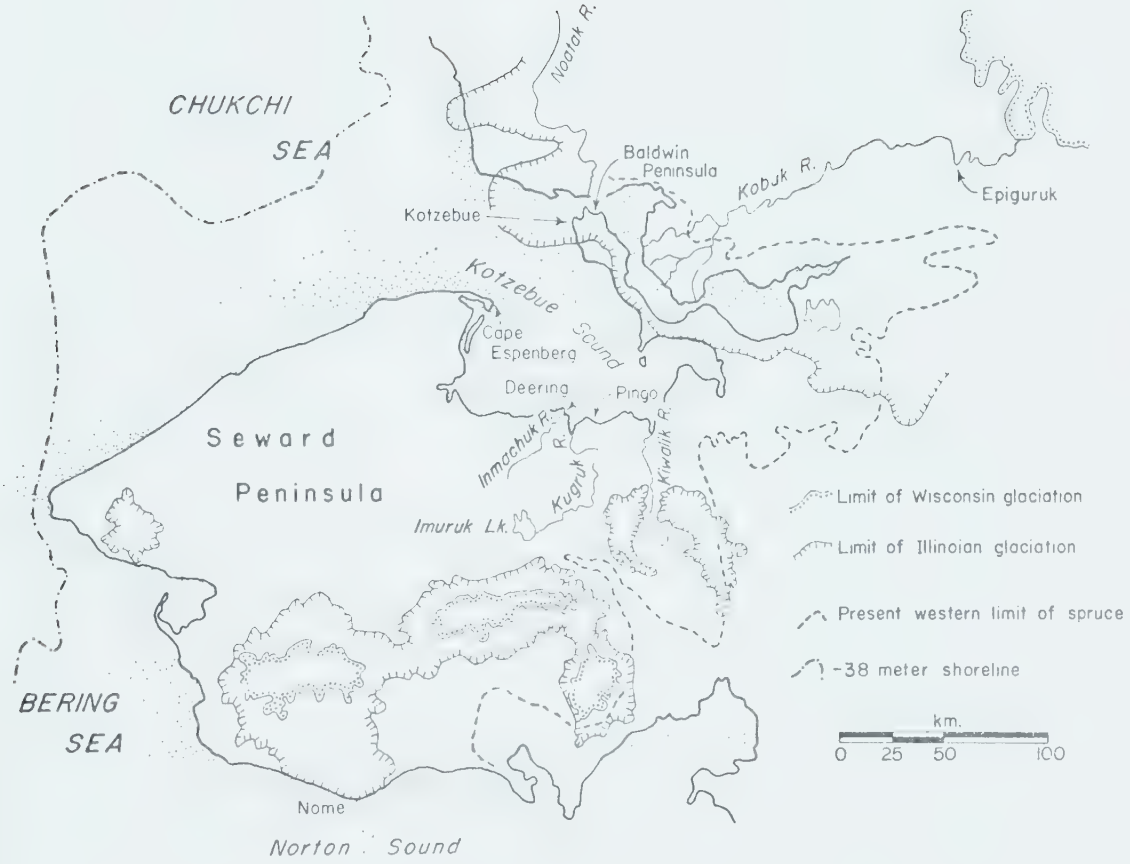

CHUKCHI
SEA
Noatak R.
Baldwin
Peninsula
Kobuk R.
Epiguruk
Kotzebue
Kotzebue Sound
Cape
Espenberg
Deering
Pingo
Seward
Peninsula
Inmachuk R.
Kiwalik R.
Kuguruk
Imuruk Lk.
BERING
SEA
Nome
Norton Sound
Limit of Wisconsin glaciation
Limit of Illinoian glaciation
Present western limit of spruce
-38 meter shoreline
km.
0 25 50 100

Figure 2

Fig. 3 Stratigraphy of the Cape Deceit Quaternary exposure: showing actual lateral and vertical relationship of named stratigraphic units and sedimentary features. Note: vertical and horizontal scales are equal.

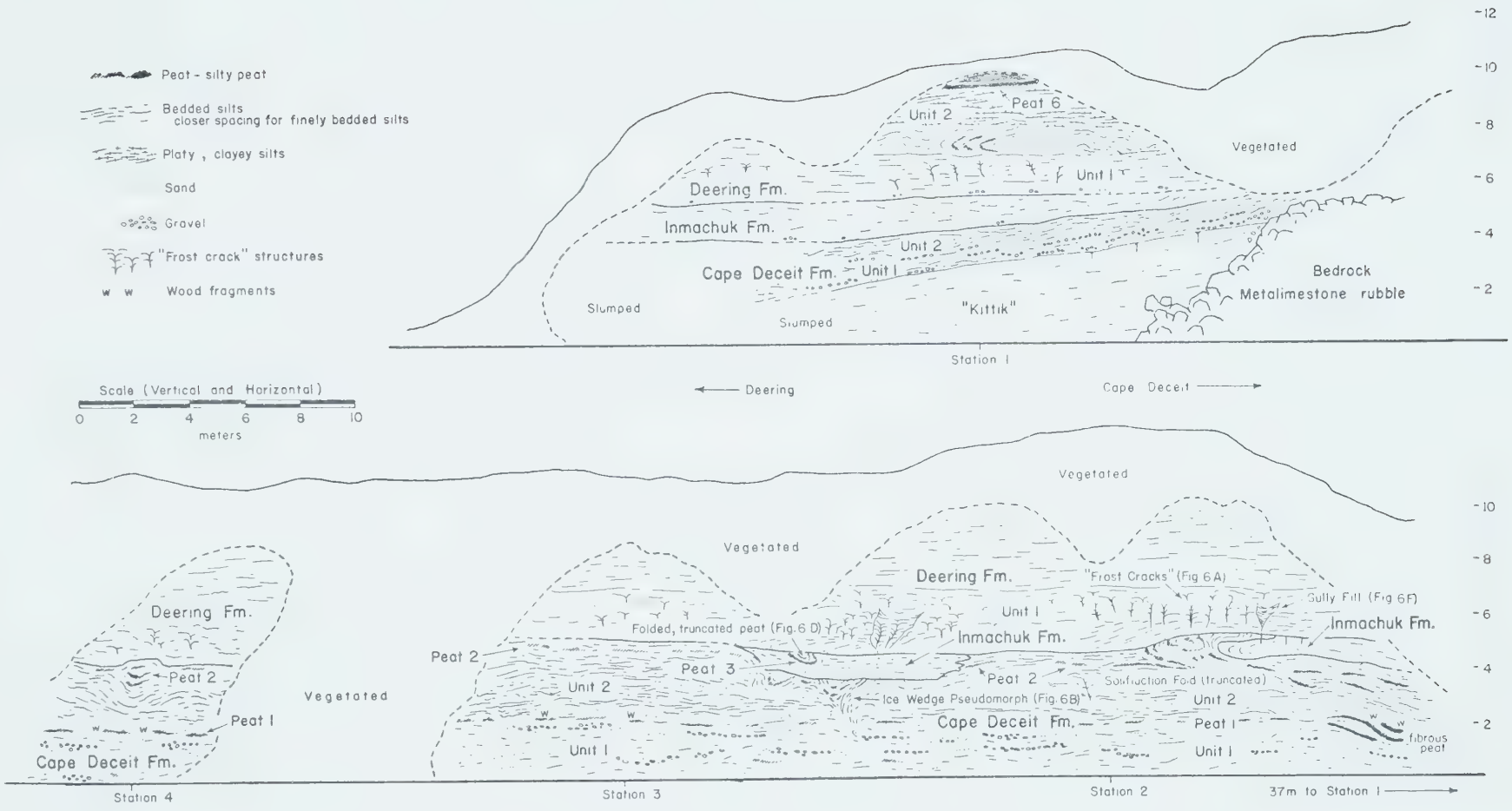

Peat - silty peat
Bedded silts
closer spacing for finely bedded silts
Platy , clayey silts
Sand
Gravel
"Frost crack" structures
w w Wood fragments
Scale (Vertical and Horizontal)
0 2 4 6 8 10
meters
Deering
Cape Deceit
Deering Fm.
Inmachuk Fm.
Cape Deceit Fm.
Unit 1
Unit 2
Peat 6
Vegetated
Slumped
"Kittik"
Bedrock
Metalimestone rubble
Station 1
Peat 1
Peat 2
Peat 3
Folded, truncated peat (Fig. 6 D)
"Frost Cracks" (Fig 6A)
Gully Fill (Fig 6F)
Ice Wedge Pseudomorph (Fig. 6B)
Solifluction Fold (truncated)
fibrous peat
Station 4
Station 3
Station 2
37m to Station 1
12
10
8
6
4
2

Figure 3

Fig. 4 Stratigraphy of the Cape Deceit Quaternary exposure: showing actual lateral and vertical relationship of named stratigraphic units and sedimentary features. Note: vertical and horizontal scales are equal.

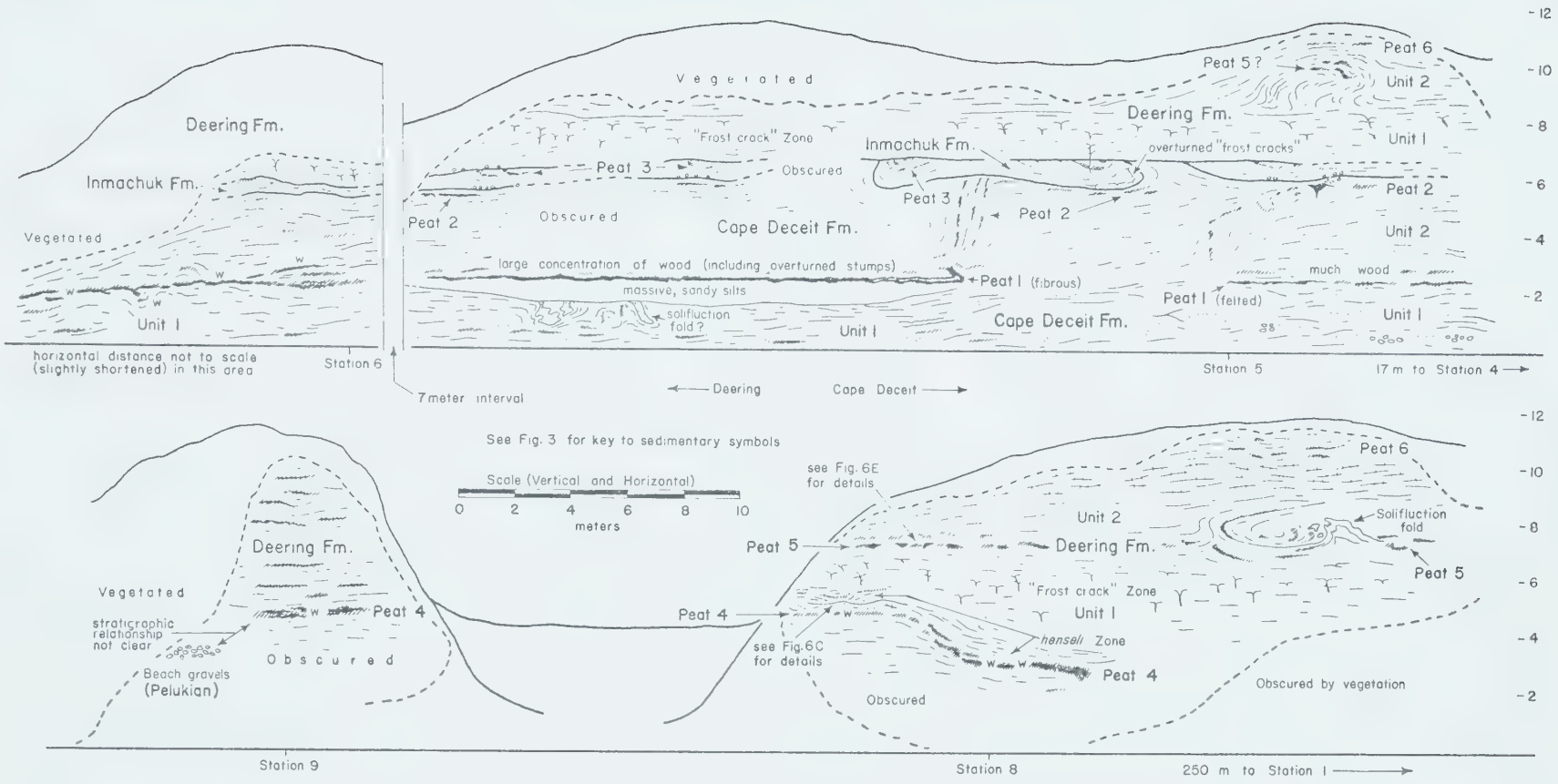
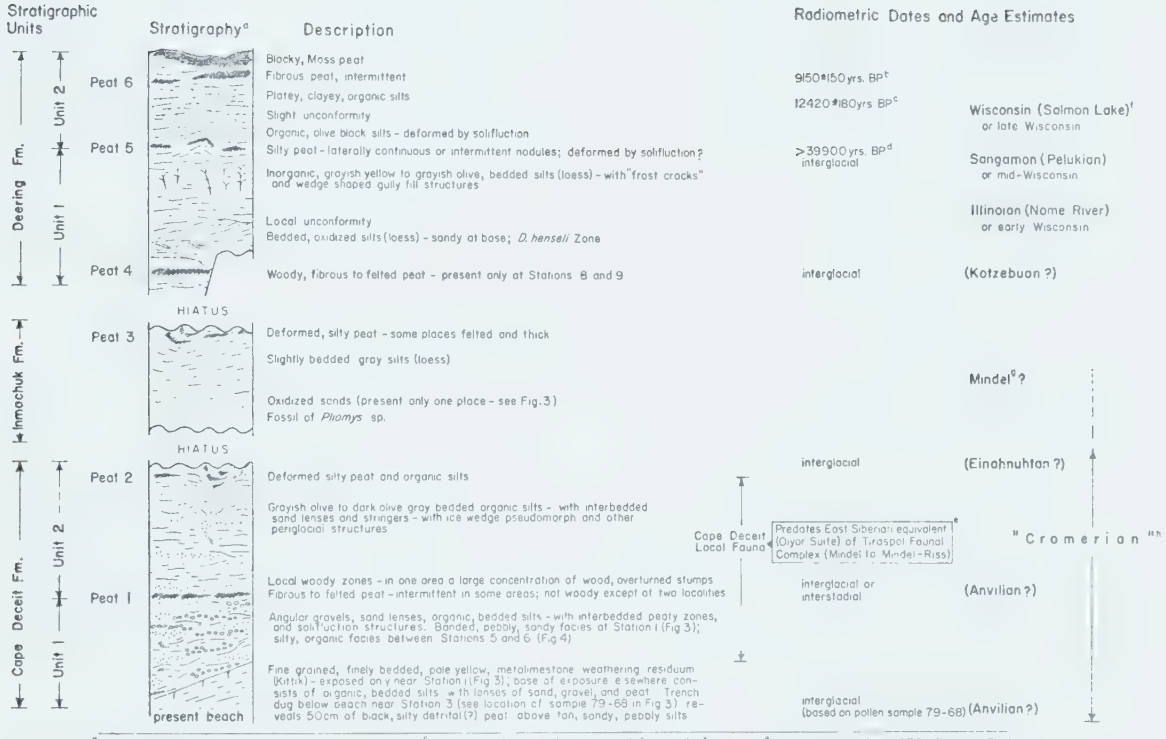

Deering Fm.
Inmachuk Fm.
Vegetated
Unit 1
horizontal distance not to scale
(slightly shortened) in this area
Station 6
7 meter interval
Vegetated
"Frost crack" Zone
Peat 3
Obscured
Peat 2
Obscured
Cape Deceit Fm.
large concentration of wood (including overturned stumps)
massive, sandy silts
solifluction fold?
Unit 1
Peat 1 (fibrous)
Peat 5?
Peat 6
Unit 2
Deering Fm.
Unit 1
Inmachuk Fm.
overturned "frost cracks"
Peat 3
Peat 2
Peat 2
Unit 2
much wood
Peat 1 (felted)
Unit 1
Cape Deceit Fm.
Station 5
17 m to Station 4
Deering
Cape Deceit
See Fig. 3 for key to sedimentary symbols
Scale (Vertical and Horizontal)
0 2 4 6 8 10
meters
Deering Fm.
Vegetated
stratigraphic relationship not clear
Peat 4
Obscured
Beach gravels (Pelukian)
Station 9
see Fig. 6E for details
Peat 5
Peat 4
see Fig. 6C for details
Peat 6
Unit 2
Deering Fm.
Solifluction fold
Peat 5
"Frost crack" Zone
Unit 1
hensell Zone
Peat 4
Obscured
Obscured by vegetation
Station 8
250 m to Station 1
-12
-10
-8
-6
-4
-2

Figure 4

Fig. 5 Generalized stratigraphy of the Cape Deceit Quaternary exposure: including descriptive notes radiometric dates, and probable correlations.



[a] For stratigraphic symbols and thickness of units see Figs 3 and 4

[b] I-4780; basal 5cm of Peat 6 at Station 1

[c] I-4781; small, autochthonous wood fragments from middle of S-6 sample interval (Station 8, Fig. 4)

[d] I-4099; Peat 5 at Station 8

[e] Vengengeim and Sher, 1970; Sher and Zazhigin, written communication, 1970

[f] Local Alaskan equivalent in parenthesis

[g] See text for explanation of use of European stage names

[h] *sensu* Zagwijn *et al.*, 1971

Figure 5

Fig. 6 Selected sedimentary features of paleoenvironmental significance and location of certain pollen sample suites. Scale: divisions on ice axe handle = 10 cm. Length of bar in B = 60 cm. Lens cap diameter in F = 3 cm.

(A) Wedge shaped dessication crack (?) typical of those within the "frost crack" zone of Unit 1 (Deering Fm.). Note change in character of wedge within sediments of the henseli Zone and banded nature of host sediments (dark tones--10YR 6/8--are ferruginous zones; medium to light tones--2.5Y 5/2--5Y 5/2--are gleyed horizons.).

(B) Ice wedge pseudomorph, Cape Deceit Fm. (Unit 2) between stations 2 and 3 (Fig. 3). Note the angular unconformity at the contact of Cape Deceit and Inmachuk formations.

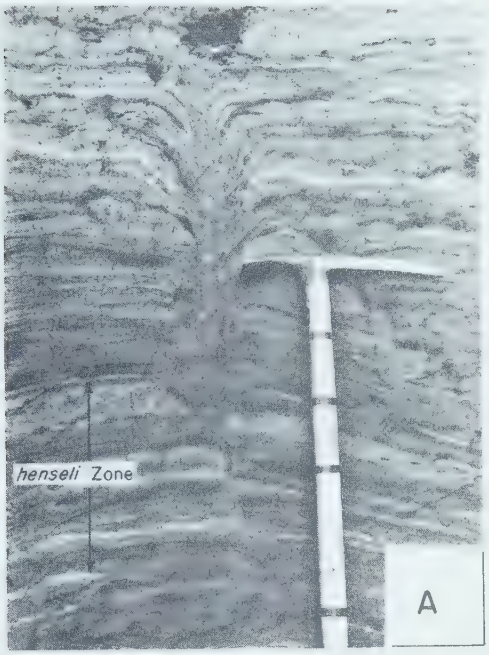
(C) Location of pollen samples immediately above Peat 4 at Station 8 (Fig. 4). 69-67--organic peaty silts associated with Peat 4; 56-69--small lens of peat within silty sands. Weakly developed congeliturbation structures visible in silty sands. 57-69--Thin peaty horizon containing some small wood fragments; 58-69--small scale cut and fill structure--organic silts; 55-69--inorganic ferruginous banded silts at base of part of Unit 1 containing "frost cracks". Samples 56-69--54-69 from henseli Zone. All samples from Deering Formation.

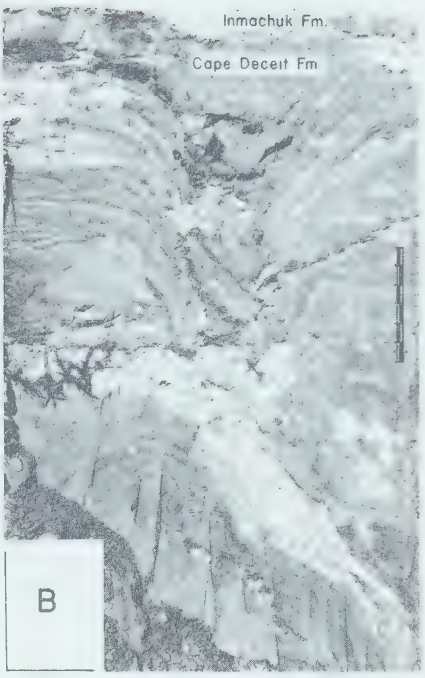
(D) Contact of Inmachuk and Deering formations, between stations 2 and 3, showing truncated fold of Peat 3.

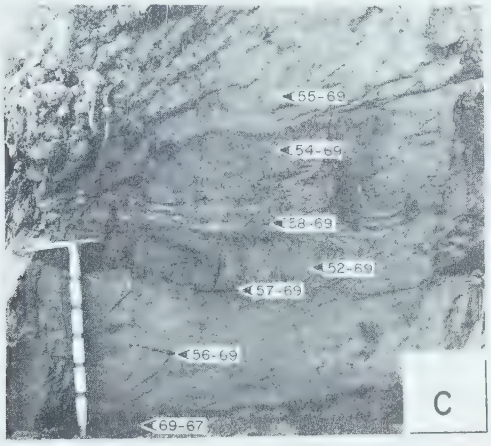
(E) Location of pollen samples from the upper part of Unit 1 and lower part of Unit 2 (Deering Fm.) at Station 8. 102-68--Peat 5; 100-68, 99-68--from peaty silts wich merge laterally with Peat 5. Note: 1. The lenticular nature of Peat 5 nodules

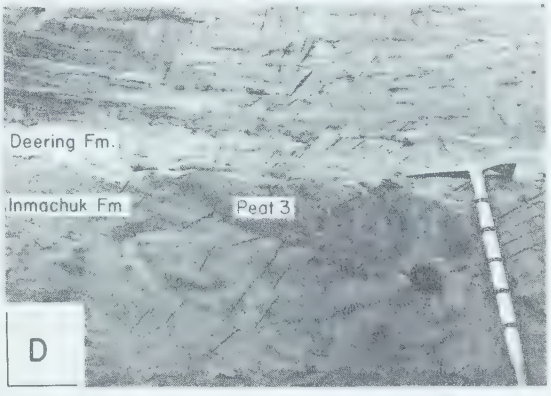
and thin bands of sand and pebbles within the nodules. 2. The weathering horizon in upper part of Unit 1 (samples 101-68 and 103-68) and 3. weakly developed "frost cracks" in Unit 1.

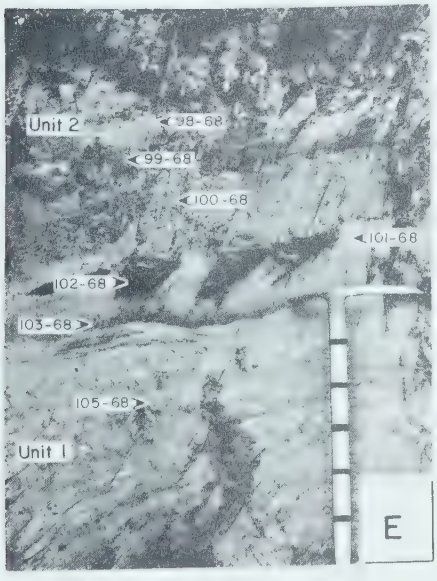
(F) Wedge-shaped gully filling from a locality near Station 2 (Fig. 3). Note nearly horizontal bedding of sediments within wedge. Cape Deceit Formation occurs above Inmachuk Formation as a result of folding presumably due to solifluction.


henseli Zone
A


Inmachuk Fm.
Cape Deceit Fm
B


55-69
54-69
53-69
52-69
57-69
56-69
69-67
C


Deering Fm.
Inmachuk Fm
Peat 3
D


Unit 2
98-68
99-68
100-68
101-68
102-68
103-68
105-68
Unit 1
E

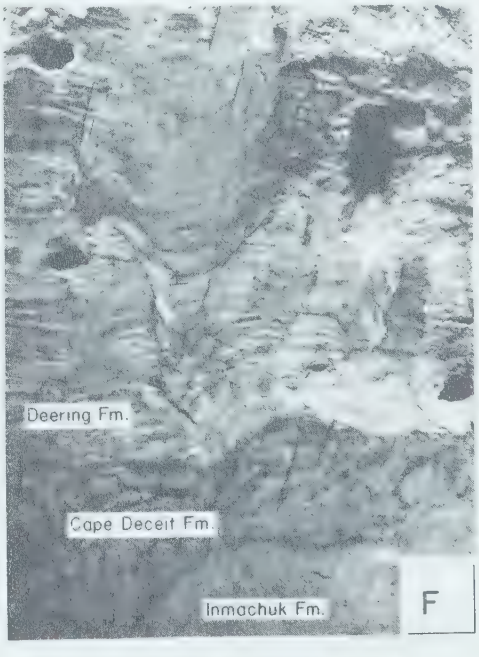

Deering Fm.
Cape Deceit Fm.
Inmachuk Fm.
F

Figure 6

Fig. 7 Location of pollen and arthropod fossil samples discussed in this paper. Compare with Figures 3 and 4.

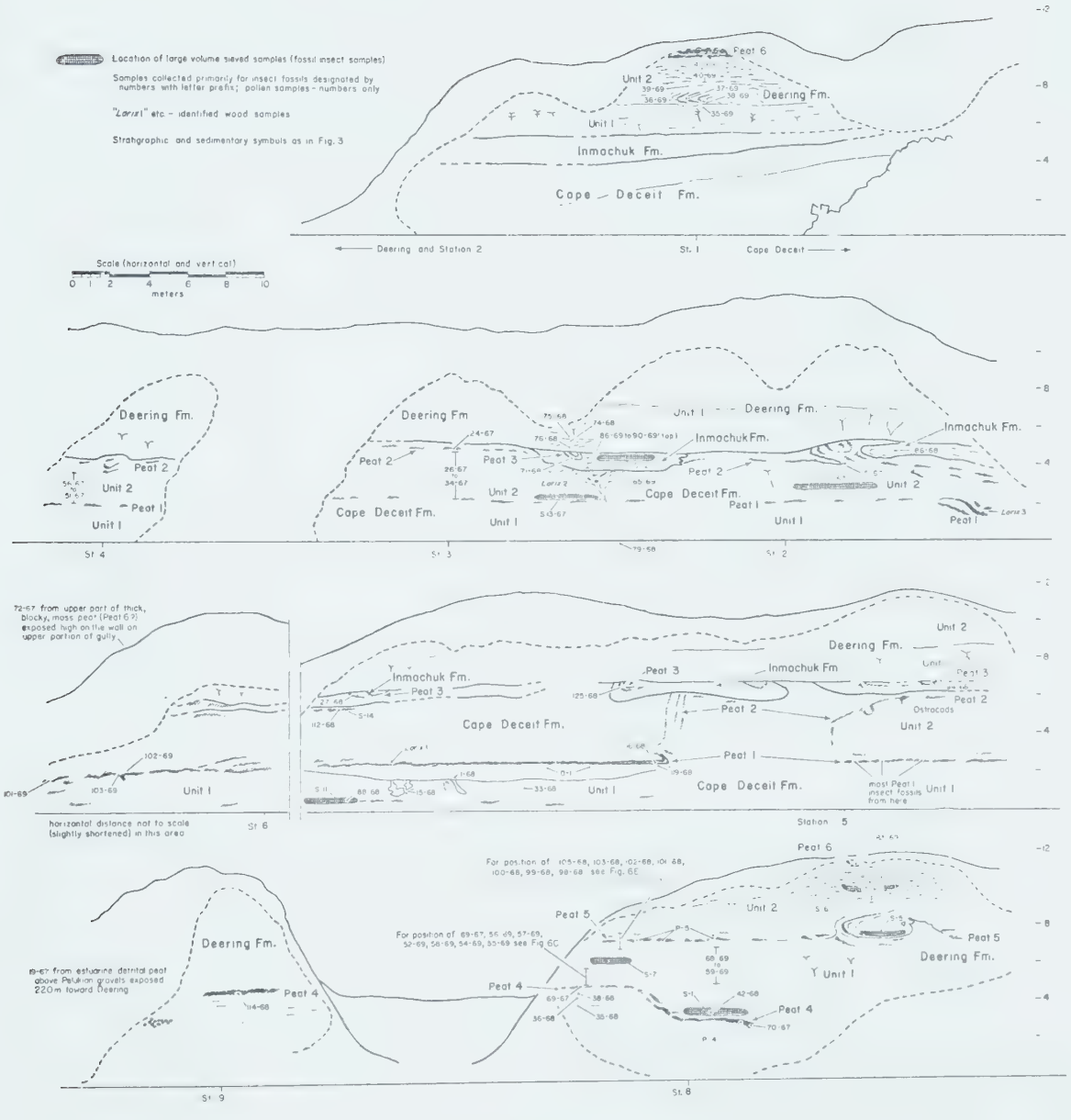

Location of large volume sieved samples (fossil insect samples)
Samples collected primarily for insect fossils designated by numbers with letter prefix; pollen samples - numbers only
"Larix1" etc. - identified wood samples
Stratigraphic and sedimentary symbols as in Fig. 3
Peat 6
Unit 2
Deering Fm.
Unit 1
Inmachuk Fm.
Cape Deceit Fm.
Deering and Station 2
St. 1
Cape Deceit
Scale (horizontal and vert cal)
0 1 2 4 6 8 10
meters
Peat 2
Peat 3
Peat 1
St 4
St 3
St 2
72-67 from upper part of thick, blocky, moss peat (Peat 6?) exposed high on the wall on upper portion of gully
horizontal distance not to scale (slightly shortened) in this area
St 6
Station 5
Ostracods
most Peat 1 insect fossils from here
For position of 105-68, 103-68, 102-68, 101-68, 100-68, 99-68, 98-68 see Fig. 6E
For position of 69-67, 56-69, 57-69, 52-69, 58-69, 54-69, 55-69 see Fig. 6C
19-67 from estuarine detrital peat above Pelukian gravels exposed 220m toward Deering
St. 9
St. 8

Figure 7

Fig. 8 Pollen diagrams. For location of individual samples and sample suites see Figure 7.

POLLEN
SPORES
Σ includes
POLLEN SAMPLES
Picea
Pinus
Abies
Larix
Alnus
Betula
Populus
Salix
Ericales
Cyperaceae
Gramineae
Artemisia
High Spine
Cichoriaceae
Rosaceae undet.
Rubus idaeus chamaemorus
Rosa acicularis chamaemorus
Potentilla fruticosa
Dryas
Rumex
Polygonum tenuicaule persicaria
Polygonum viviparum
Cerastium undet.
Caryophyllaceae undet.
Saxifraga
Ranunculus acris
Ranunculus undet.
Ranunculaceae undet.
Thalictrum
Ranunculaceae undet.
Saxifragaceae undet.
Parnassia
Umbelliferae
Geranium
Polemonium
Boraginaceae
Polemonium-Trigonocarpum
Liliaceae
Vaccinium oxycoccus
Liliaceae undet. pollen
Sphagnum
Indet. pollen
Triletes undet.
Botrychium
Woodsia
Polypodiaceae undet.
Equisetum
Lycopodium
Lycopodium selago
Selaginella
Rosaceae
Compositae
Fig. 7 - St 2-St 3
Unit 2
Peat 2
Peat 3
Unit 2
Fig. 7 - St 3
Peat 1
Unit 1
Peat 1
Unit 1
FORMATION
INMACHUK
FORMATION
DECIT
CAPE
Stratigraphic symbols as in Fig. 3
% of Σ (except for "Indet. Pollen" category)
+ = Named taxon present, but 1% or less

Figure 8

Fig. 9 Pollen diagrams. For location of individual samples and sample suites see Figure 7.

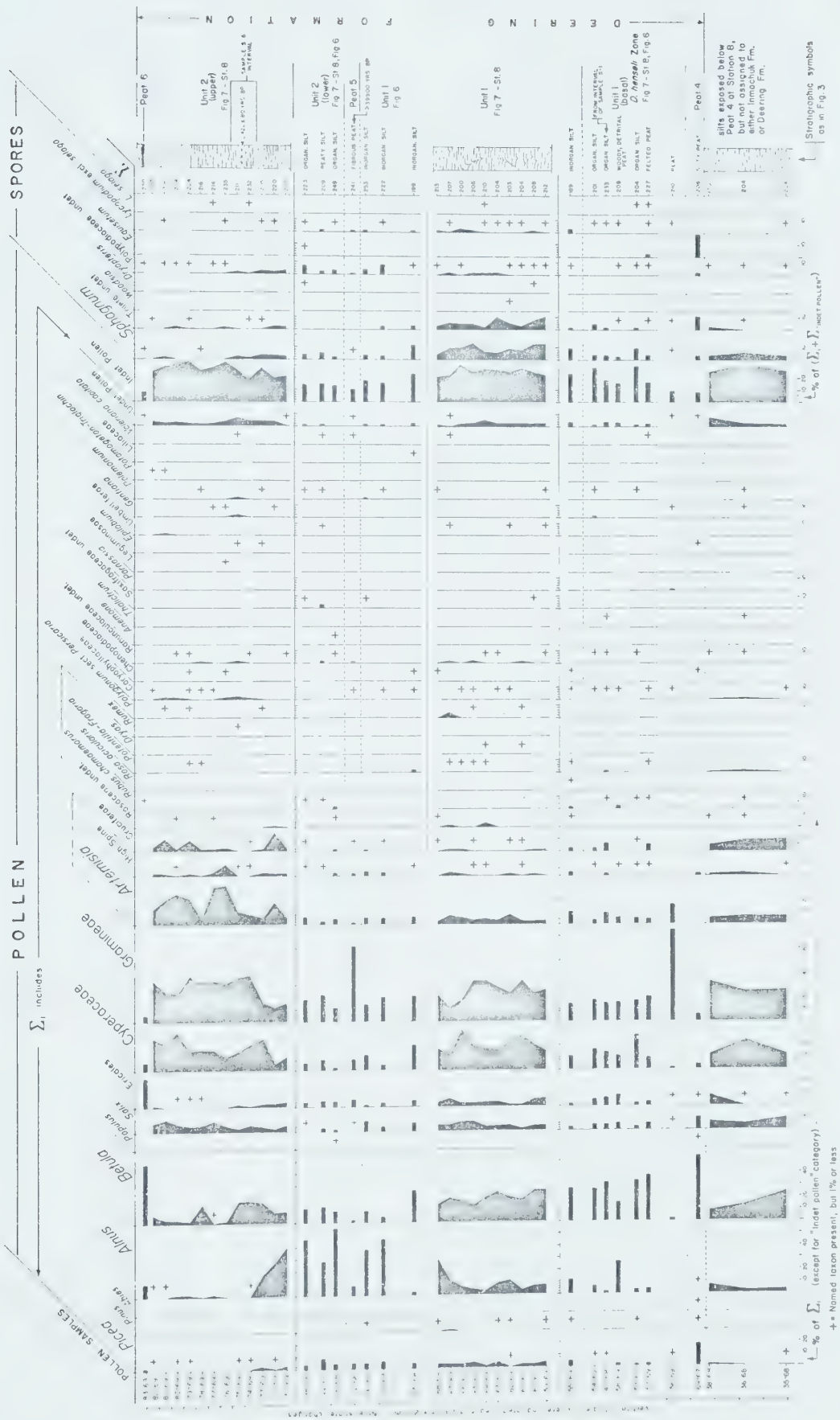

POLLEN
SPORES
Σ1 includes
POLLEN SAMPLES
Picea
Pinus
Alnus
Betula
Populus
Salix
Ericales
Cyperaceae
Gramineae
Artemisia
High Spine
Quadrilarge
Rosaceae undet.
Rubus chamaemorus
Rosa acicularis
Polygonum viviparum
Rumex
Cruciferae
Caryophyllaceae
Chenopodiaceae
Ranunculaceae undet.
Aconitum
Thalictrum
Saxifragaceae undet.
Rorippa
Leguminosae undet.
Epilobium
Geum
Potentilla
Thamnocalyx
Liliaceae
Shepherdia canadensis
Lycopodium undet.
Equisetum
Sphagnum
Monolete undet.
Trilete undet.
Pollen undet.
Spore undet.
Peat 6
Unit 2 (upper) Fig 7 - St. 8
Peat 5
Unit 2 (lower) Fig 7 - St. 8, Fig 6
Unit 1 Fig 6
Unit 1 Fig 7 - St. 8
Peat 4
Unit 1 (base)
Zone
Fig 7 - St. 8, Fig 6
ORGAN. SILT
PEATY SILT
INORGAN. SILT
PELTED PEAT
WOODY DETRITAL PEAT
silts exposed below Peat 4 at Station 8, but not assigned to either Inmachuk Fm. or Deering Fm.
Stratigraphic symbols as in Fig. 3
% of Σ1 (except for "Inder pollen" category)
+ = Named taxon present, but 1% or less
% of (Σ1 + Σ2 + Σ3 INDET POLLEN)

Figure 9

Fig. 10 Pollen diagrams. For location of individual samples and sample suites see Figure 7.

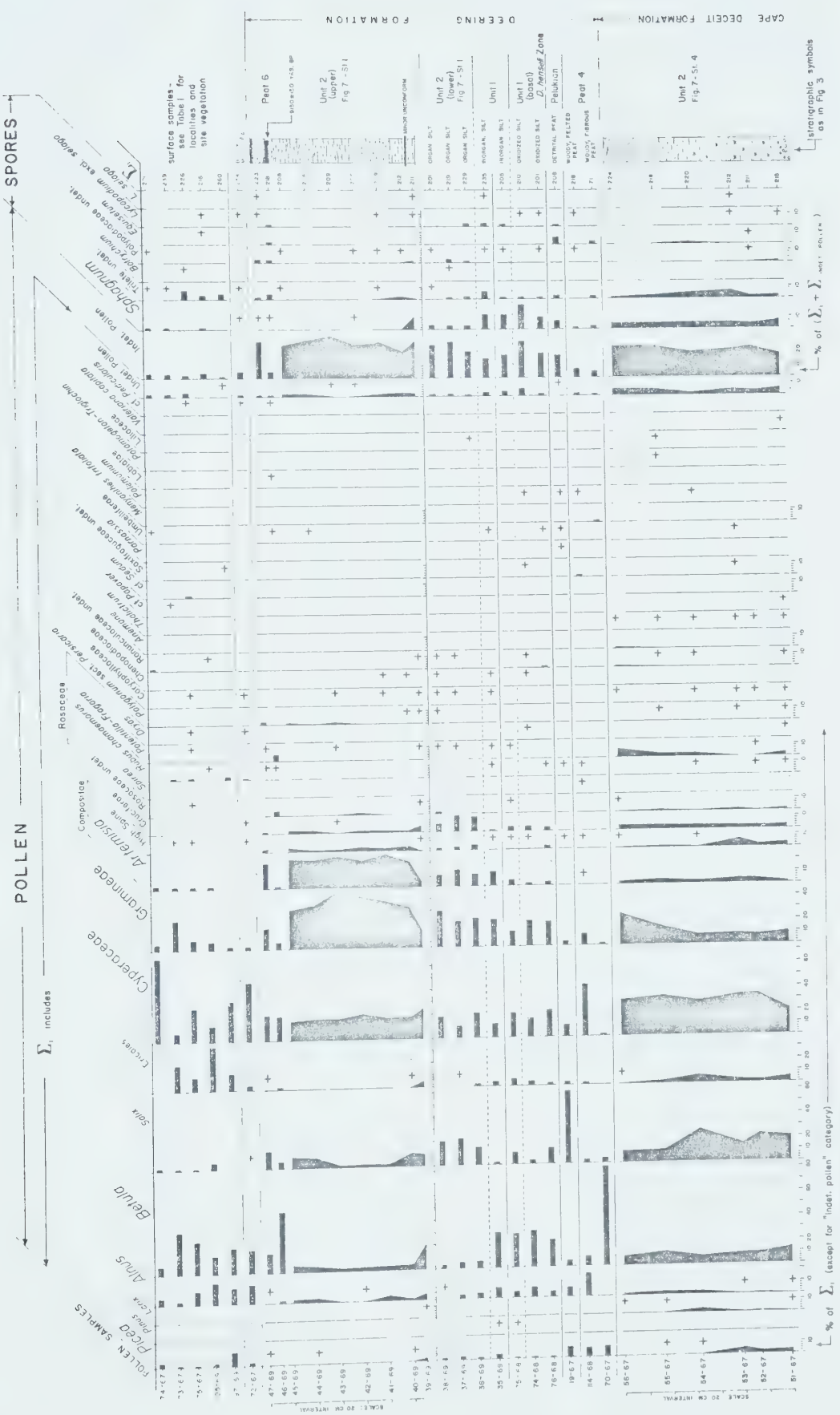

POLLEN
SPORES
Σ1 includes
POLLEN SAMPLES
Picea
Pinus
Larix
Alnus
Betula
Salix
Ericales
Cyperaceae
Gramineae
Artemisia
Rosaceae
Composite
surface samples - see Table I for localities and site vegetation
Peat 6
Unit 2 (upper) Fig 7 - St 1
Unit 2 (lower) Fig 7 - St 1
Unit 1
Unit 1 (basal)
D. hensoff Zone
Peat 4
Unit 2 Fig 7 - St 4
DEERING FORMATION
CAPE DECEIT FORMATION
stratigraphic symbols as in Fig 3
+ = Named taxon present, but 1% or less

Figure 10

Fig. 11 Generalized pollen diagram from Imuruk Lake (modified from Colinvaux, 1964 and Colbaugh, 1968). Dates for zonal boundaries in Core I are from Colbaugh (1968). Note: Core I samples are lacustrine silts and clays; whereas Zone M samples are autochthonous and allochthonous peats.

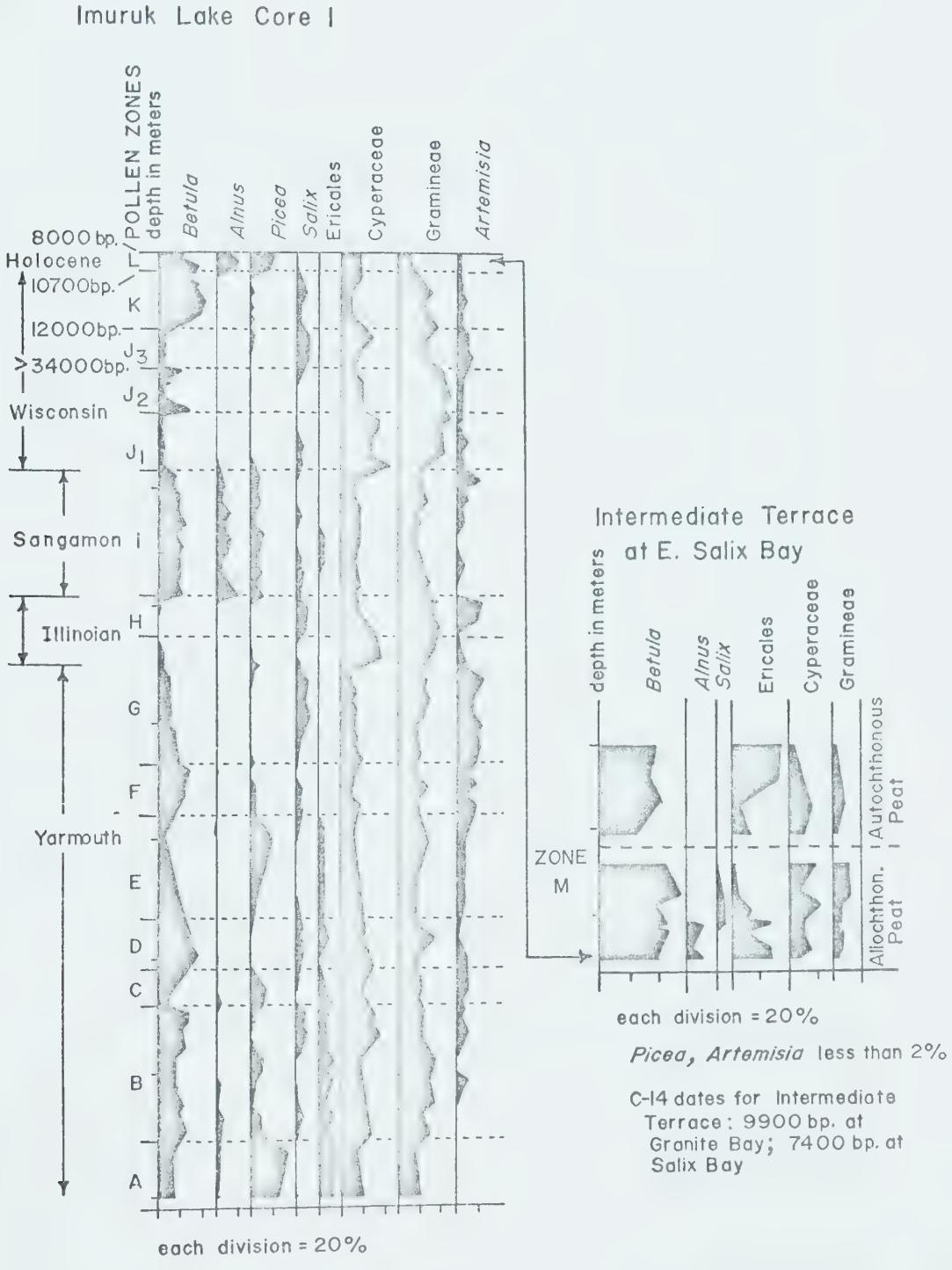

Imuruk Lake Core I
POLLEN ZONES
depth in meters
Betula
Alnus
Picea
Salix
Ericales
Cyperaceae
Gramineae
Artemisia
8000 bp.
Holocene
10700bp.
12000bp.
34000bp.
Wisconsin
Sangamon i
Illinoian
Yarmouth
K
J3
J2
J1
H
G
F
E
D
C
B
A
each division = 20%
Intermediate Terrace
at E. Salix Bay
depth in meters
Betula
Alnus
Salix
Ericales
Cyperaceae
Gramineae
ZONE
M
Autochthonous
Peat
Allochthon.
Peat
each division = 20%
Picea, Artemisia less than 2%
C-14 dates for Intermediate
Terrace: 9900 bp. at
Granite Bay; 7400 bp. at
Salix Bay

Figure 11

Fig. 12 Plant macrofossils from Quaternary sediments of Cape Deceit.

See Figure 7 for stratigraphic provenience of samples.

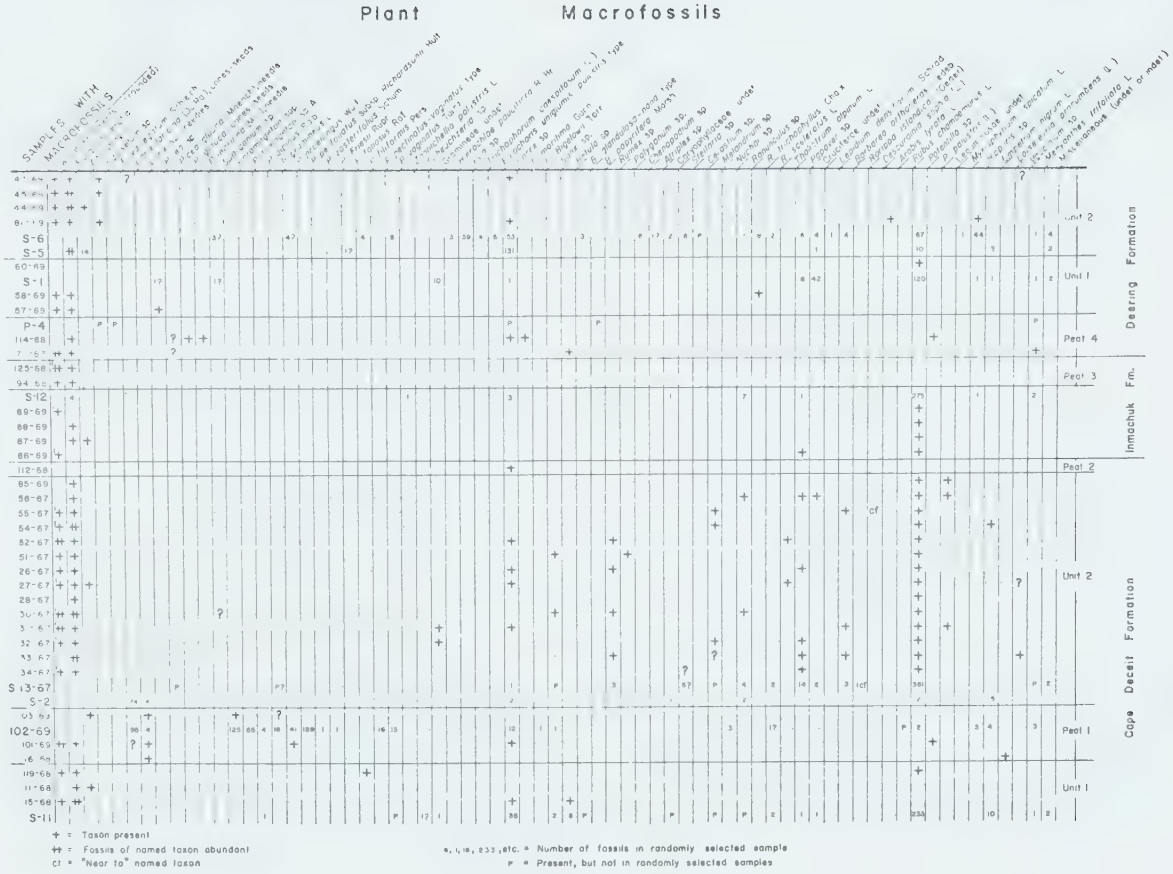

Plant Macrofossils
SAMPLES WITH MACROFOSSILS
S-6
S-5
S-1
P-4
S-12
S-2
S-11
Unit 2
Unit 1
Peat 4
Peat 3
Peat 2
Peat 1
Dearing Formation
Inmachuk Fm.
Cape Deceit Formation
+ = Taxon present
++ = Fossils of named taxon abundant
Cf = "Near to" named taxon
e.g., 18, 233, etc. = Number of fossils in randomly selected sample
P = Present, but not in randomly selected samples

Figure 12

Fig. 13 Photos of selected plant macrofossils. (A) Female cone, Picea glauca (Moench), Peat 4 (Deering Fm., Fig. 4, St. 9) (B) Winged seed, Picea glauca, Peat 4 (Deering Fm., Fig. 4, St. 9). Derived from a cone of the same size as the one in A.

(C) Female cone, Larix laricina (Du Roi), Peat 1 (Cape Deceit Fm., Fig. 3, St. 6).

(D) Winged seed, Larix laricina, Peat 1 (Cape Deceit Fm., Fig. 3, St. 6).

(E) Achene, Thalictrum alpinum L., residue of pollen samples 52-67 (Cape Deceit Fm., Unit 2).

(F) Achene, Ranunculus trichophyllus Chaix., sample S-6 (Deering Fm., Unit 2).

(G) Seed, Barbarea orthoceras Ledeb.?, sample S-6 (Deering Fm., Unit 2).

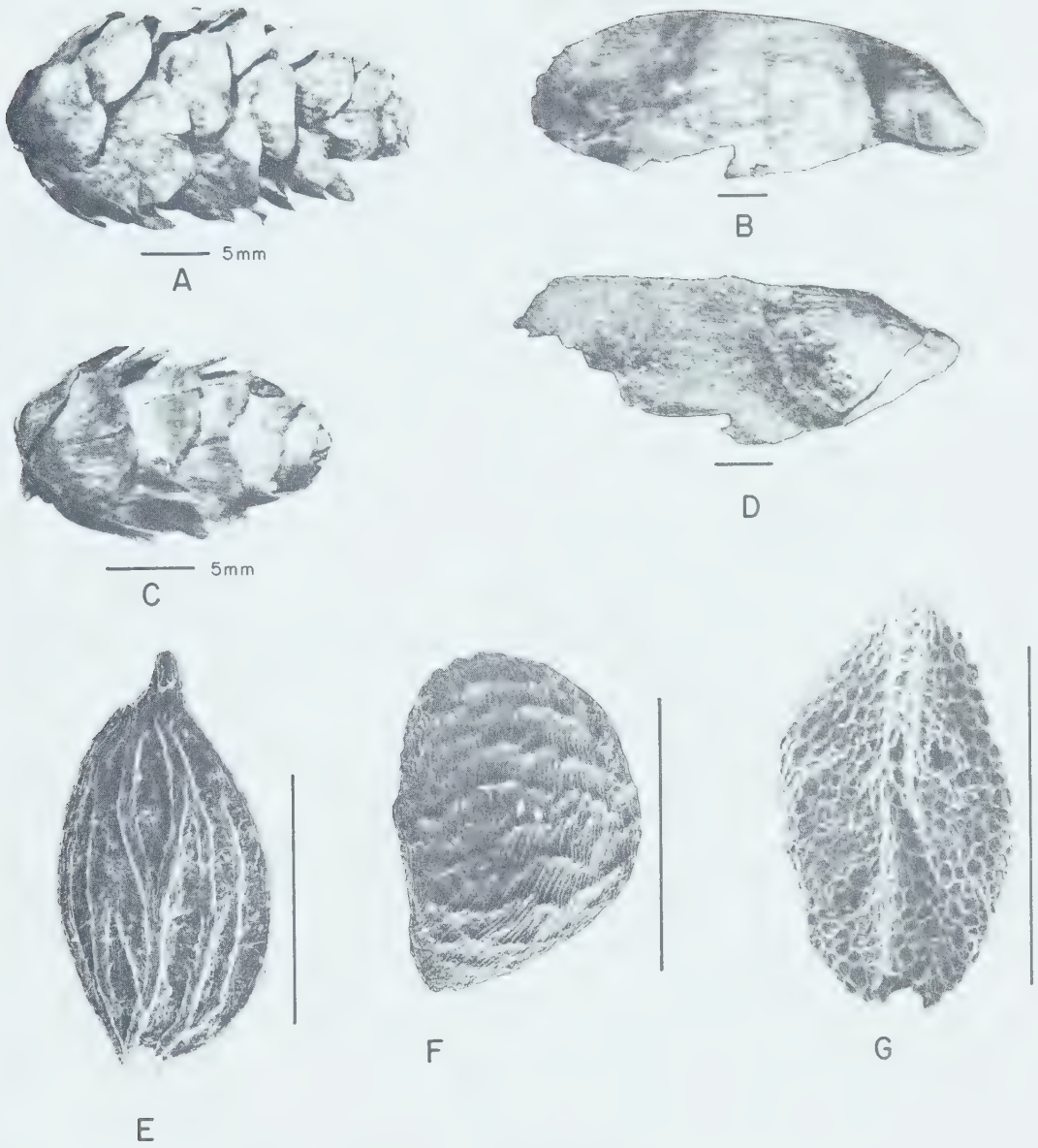


Figure 13

Fig. 14 Miscellaneous animal macrofossils from pollen sample residues and macrofossil samples other than those listed in Table 3.

Miscellaneous
Animal
Macrofossils
Crustacea
Insecta
SAMPLES WITH MACROFOSSILS
Bryozoa
Mollusca
Ostracoda
Arachnida (Acari)
Coleoptera
Diptera
Hymenoptera
Unit 2
Peat 6
Unit 2
Peat 5
Unit 1
see Fig 7 St 8
Peat 3
Peat 2
Unit 2
Peat 1
Unit 1
Formation
Deering
Cape Deceit Formation
Innachuk Fm
+ = Taxon present
cf. = "Near to" named taxon
i, for additional fossils see Table 3
Mollusca identified by L. Kalas
Ostracoda identified by L. D. Delorme

Figure 14

Fig. 15 Scanning Electron Microscope photos of selected Arthropod fossils.

(A) Pronotum, Amara Alpina Payk., sample S 13-67 (Cape Deceit Fm., Unit 2).

(B) Pronotum, Amara bokeri Csiki, sample S 13-67 (Cape Deceit Fm., Unit 2).

(C) Pronotum, Pterostichus nearcticus Lth., sample S-6 (Deering Fm., Unit 2).

(D) Left side view of partially articulated specimen, Ceutorhynchus sp. samples S 10-67 (Cape Deceit Fm., Unit 2). Fossil indicates excellent state in preservation of some of oldest insect fossils from the Quaternary exposure.

(E) Head, Leptothorax canadensis Prov., Peat 4 (Deering Fm., Fig. 4, St. 8)

(F) Articulated left and right elytra, Subhaida sp., sample S-1 (Deering Fm., henseli Zone).

(G) Left elytron, Morychus aeneolus (Lec.)?, sample S-6 (Deering Fm., Unit 2).

(H) Oribatid mite, dorsal view, Ameronothrus sp., Peat 4 Deering Fm., Fig. 4, St. 8).

(I) Left elytron, Cassida flaveola Thunb., Peat 1 (Cape Deceit Fm., Fig. 3, near St. 2).

(J) Left male palpus, Tarentula pictilis (Emerton), sample S-5 (Deering Fm., Unit 1).

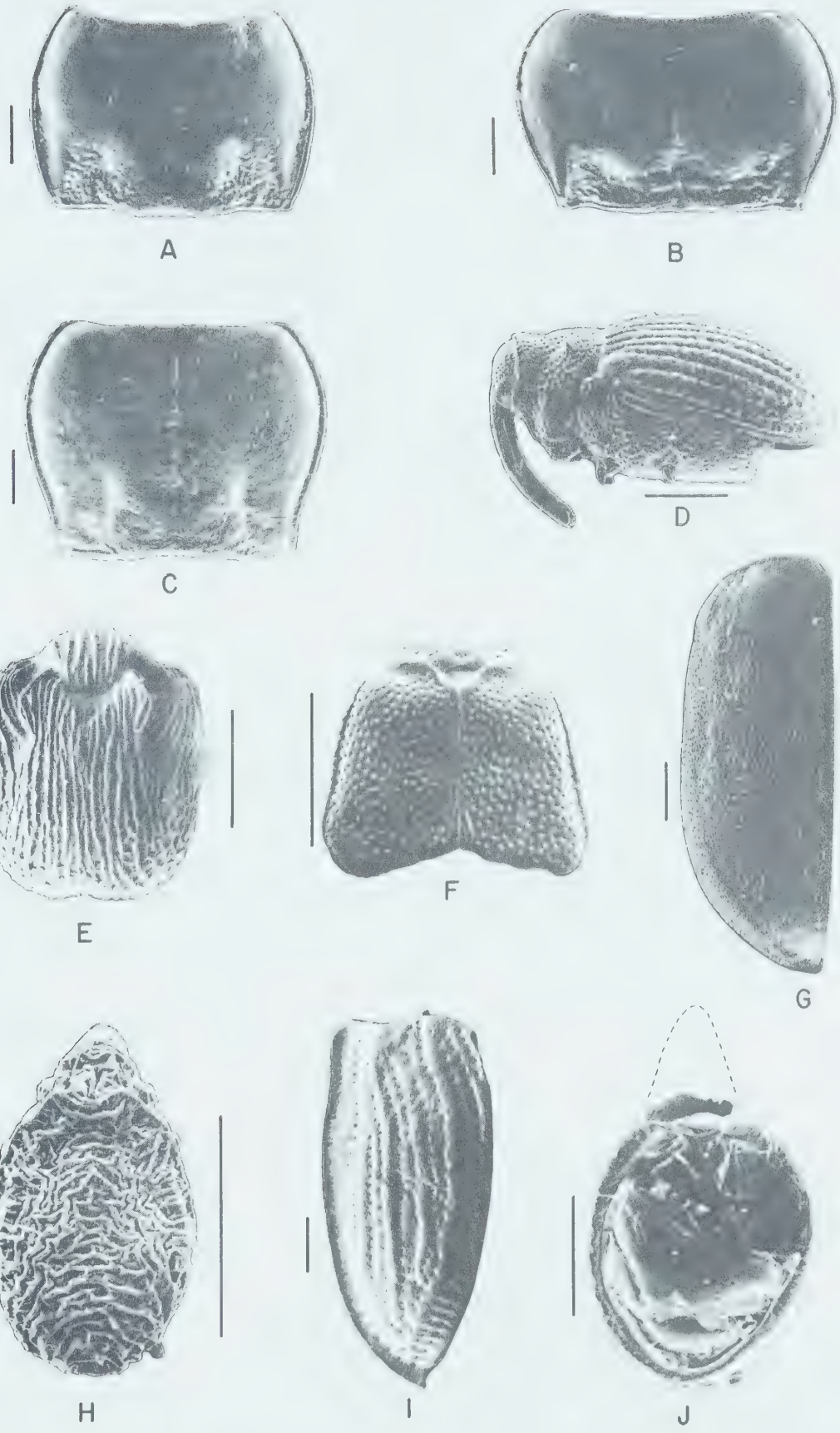


Figure 15

Fig. 16 Dorsal and lateral views of male genitalia of Chrysolina species. "flg." = Flagellum.

(a) Chrysolina cf cavigara (Sabhlb.), sample S 13-67 (Cape Deceit Fm., Unit 2).

(b) Chrysolina cf rugilabris (Fald.) sp. C, sample S-1 (Deering Fm., Unit 1).

(c) Chrysolina cf rufilabris (Fald.), sp. B, sample S-6 (Deering Fm., Unit 2).

(d) Chrysolina rufilabris (Fald.), contemporary specimen, V. Udukunsk, Odenvall, (in collections of Zoological Museum, University of Helinski).

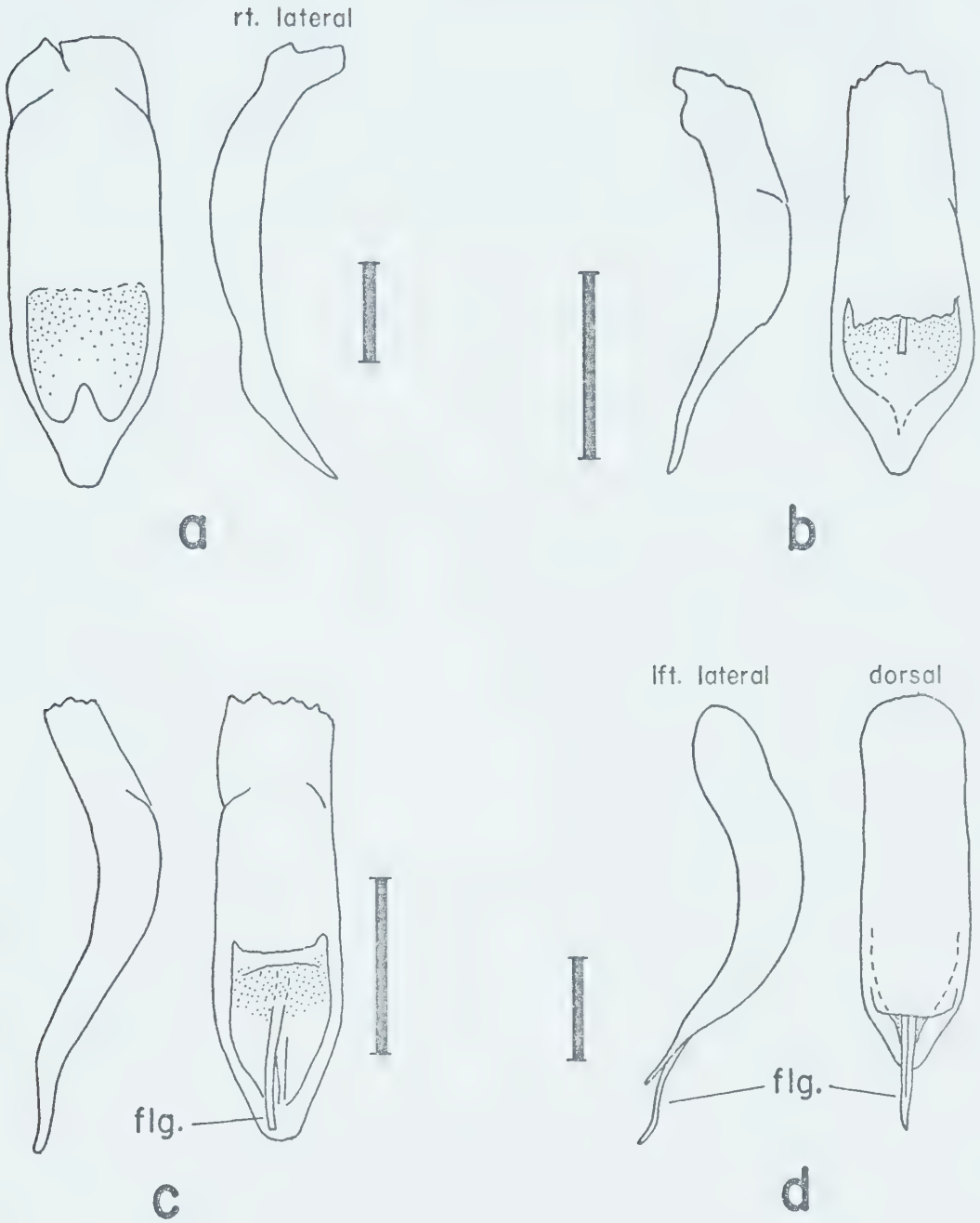


Figure 16

Fig. 17 Inter-assemblage comparisons of elytral size and wing in Tachinus apterus. Assemblages S 13-67 and S 10-67 from Cape Deceit Fm. (Unit 2), S-12 from Inmachuk Fm., S-5 and S-6 from Deering Fm. (Units 1 and 2 respectively). See Figure 5 and text for probable age of the assemblages. Line A: regression of length on width for S-6 elytra (n = 73, Y = 15.9 + 0.55X). Line B: regression of length on width for S 1-67 elytra (n = 76, Y = 18.0 + 0.45X). "st." in illustration = stigma.

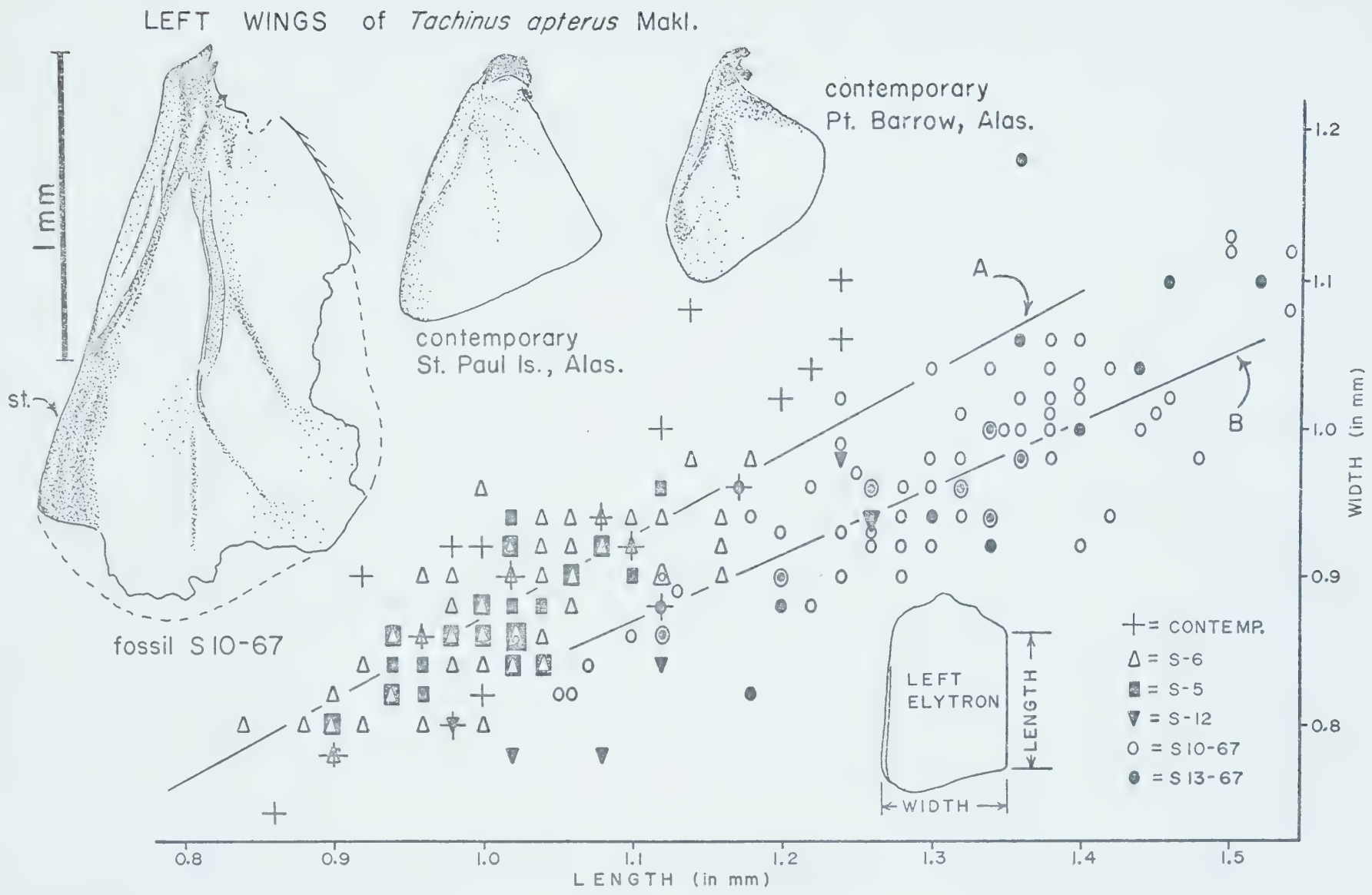

LEFT WINGS of *Tachinus apterus* Makl.
1 mm
st.
fossil S 10-67
contemporary
St. Paul Is., Alas.
contemporary
Pt. Barrow, Alas.
A
B
LEFT
ELYTRON
LENGTH
WIDTH
+ = CONTEMP.
Δ = S-6
■ = S-5
▼ = S-12
O = S 10-67
● = S 13-67
WIDTH (in mm)
1.2
1.1
1.0
0.9
0.8
0.8
0.9
1.0
1.1
1.2
1.3
1.4
1.5
LENGTH (in mm)

Figure 17

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The Cape Deceit Fauna—Early Pleistocene Mammalian Assemblage from the Alaskan Arctic

R. D. GUTHRIE[1] AND JOHN V. MATTHEWS, JR.[2]

Received May 17, 1971

Pleistocene exposures located near Cape Deceit on the south shore of Kotzebue Sound (Alaska) contain a complex sequence of organic sediments which have yielded fossil vertebrates of taxonomic, evolutionary, and zoogeographic significance. Cape Deceit Local Fauna from the Cape Deceit Formation, lowermost of three major stratigraphic units recognized at the site, contains representatives of the genera *Canis, Rangifer, Cervus, Ochotona, Lemmus, Microtus, Pliomys,* and a newly described genus and species, *Predicrostonyx hopkinsi*—predecessor of the extant genus *Dicrostonyx*. In addition to *P. hopkinsi,* new species of *Ochotona, Pliomys,* and *Microtus* are described from the Cape Deceit Local Fauna. The stage of evolution of *Microtus deceitensis* sp. n. and *P. hopkinsi* sp. n. indicate that the Cape Deceit Formation is at least of pre-Cromerian age. This assumption is substantiated by the stratigraphy of the overlying Inmachuk and Deering formations, fossils from these units (including *Dicrostonyx torquatus* and *D. henseli*), and C-14 dates. The Cape Deceit Local Fauna, therefore, contains the earliest North American record of several of the included genera in addition to the only North American record of *Pliomys*.

Stratigraphic features at the exposure indicate that the Cape Deceit Local Fauna mammals lived in a treeless (tundra) environment showing that the contemporary tundra mammalian fauna has a lengthy arctic-adapted evolutionary history. We postulate the existence in northeastern Eurasia and Alaska of a Pleistocene–Recent "Beringian" mammalian realm which has at times contributed to the fauna of more southern regions of the Palaearctic and Nearctic. The fact that this southern movement of arctic-adapted or arctic-derived Beringian mammals occurred at different times in Europe and North America (interpreted by some as indicating the existence of a "Beringian filter-bridge") is, we think, due largely to differences of continental physiography and Pleistocene geography south of the Beringian area.

INTRODUCTION

Because of the paucity of early to middle Pleistocene mammal fossils from arctic areas, it has been difficult to document the evolution and paleoecology of arctic faunas and particularly their relationship with faunas of more southern regions. Lacking such evidence, paleontologists and zoogeographers have generally relied, for such inferences, on the homotaxial relationships of mammalian fossils from central North Americal and Eurasia. Now, however, sites in northeastern Siberia (Sher, 1969) and western Alaska (this paper) have begun to provide early to middle Pleistocene fossils of tundra-adapted mammals. In Alaska this new information comes from an exposure near the town of Deering on the north coast of the Seward Peninsula (Fig. 1, Fig. 11). This site—the Cape Deceit exposure—has been mentioned in press

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on several occasions (Karlstrom, *et al.*, 1964; McCulloch, 1967; Hopkins *et al.*, 1971), but has never been studied in detail nor have attempts been made there to collect vertebrate and other terrestrial fossils by screen-washing techniques. It became apparent in our initial study of the exposure using such techniques that it contained an abundance of mammal fossils among which are several new taxa. These provide evidence for the existence during Pleistocene time of a large intercontinental arctic mammalian realm with its own complex evolutionary unity. The number of fossils from the oldest levels of the exposure make it possible to comment on early Pleistocene mammalian community structure while certain sedimentary features provide information on paleoautecology. Detailed stratigraphic information presented here records the state of the ever-changing exposure at the time when mammalian collections were made and also provides some independent evidence for the age of the lowest mammal-bearing sediments.

The Cape Deceit locality is located within a region of shrub tundra and continuous permafrost. The nearest spruce trees occur approximately 40 km to the east of the site; however, continuous spruce woodland is no closer than approximately 75 km (Fig. 11). Mean annual temperature is within the range -4 to $-8°C$; mean annual precipitation is within the range 150 to 300 mm (Hulten, 1968). Local bedrock consists primarily of Paleozoic metalimestone (outcropping at Cape Deceit), Paleozoic schists, and Cenozoic (Pliocene) basalts (Hopkins *et al.*, 1971). Surficial sediments in the Deering area consist of loess on the interfluves, frost rubble on slopes where bedrock is exposed; terrace deposits composed of alluvium and colluvial silts near the larger river valleys (i.e., Inmachuk River); and interstratified marine and terrestrial sediments near the coast (Karlstrom *et al.*, 1964).

The Cape Deceit locality is comprised of intermittent fresh exposures along approximately 250 meters of shoreline between Deering and Cape Deceit (Fig. 1). Figures 2 and 3 illustrate the true vertical and horizontal relationship of the various stratigraphic units recognized there; Fig. 4 is a composite section with brief lithologic descriptions. To facilitate descussion of the complex stratigraphy of the exposure, stations were established along the length of the exposure and are referred to in the text below and in Figs. 2 and 3.

STRATIGRAPHY

Cape Deceit Formation

Occurring in the basal 4–5 meters of the Cape Deceit exposure in the area between the bedrock outcrop near Station 1 and Station 6 (Figs. 2 and 3), this stratigraphic unit consists primarily of olive gray to greenish silts with an admixture of angular gravels, sands, and peat. The lower limit is obscured by slump and contemporary beach gravels. The upper limit is in angularly unconformable contact with either the overlying Inmachuk or Deering formations. The Cape Deceit Formation is distinguished from these units, especially near the contact, by its darker, more compact and organic sediments. Several minor sedimentary units are recognized within this formation. These are:

Kittik. This unit (Fig. 2, Station 1), the pale yellow yellow sediments of which are valued by the Eskimos for the preparation of hides, consists entirely of silt-size to fine-sand-size, angular metalimestone fragments. At the contact with bedrock, larger metalimestone fragments are interbedded with the Kittik. This, in addition to the angularity and lithology of the Kittik sediments, attests to their local derivation; moreover, since few if any of the grains show signs of chemical weathering (surface discoloration or solution pitting), mechanical weathering such as might occur in a periglacial environment

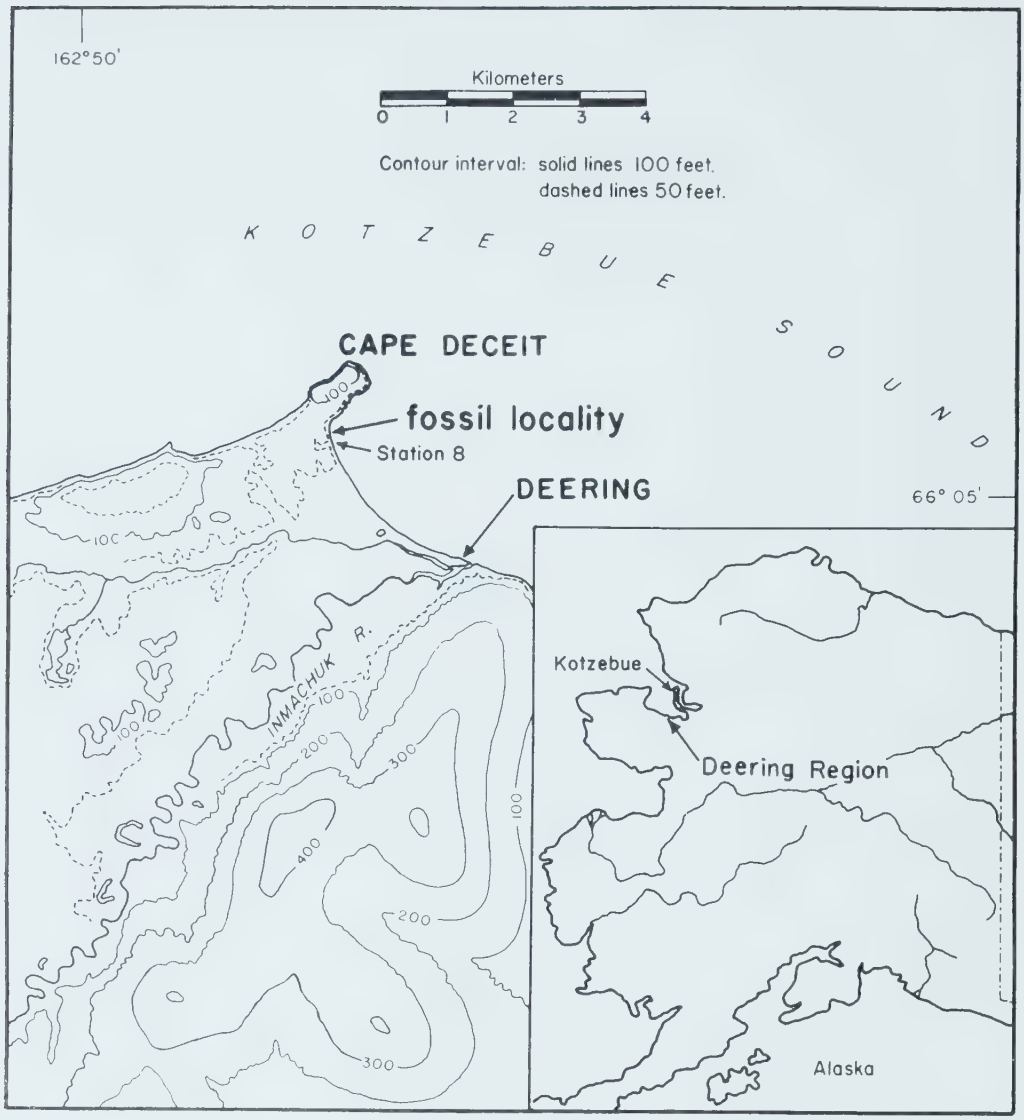


FIG. 1. Location of Cape Deceit Fossil Locality, Deering Region, Alaska.

seems to be the most probable mode of formation.

A few small vertical cracks (frost or desiccation cracks) occur within the Kittik unit at the contact with overlying solifluction deposits (Unit 1). Although the cracks are filled by silts of the overlying unit they do not extend upward into that unit. This and the fact that none of the overlying silts and gravels are incorporated in the Kittik strongly suggests that the two units—Kittik and Unit 1—were deposited at different times.

Unit 1. Occurring at the base of the exposures in all areas except at Stations 8 and 9, Unit 1 is characterized by a prominent facies change from banded silts, sands, and angular gravels near Station 1 (Fig. 2) to inorganic silts with interbedded partly detrital peaty zones and only isolated lenses of coarse sand or angular gravels near Station 5 (Fig. 3). A lens of massive, dark olive

gray (2.5 GY 4/1) sandy silt, likely the result of rapid colluvial deposition, occurs unconformably above bedded silts and peats and immediately below Peat 1 in the area between Stations 5 and 6 (Fig. 3). An oxidized zone similar to a soil occurs at the contact of the sandy silt and Peat 1 where the latter is abruptly deformed. This is thought to be the result of groundwater movement during thawing and slumping of the overlying sediments in Unit 2.

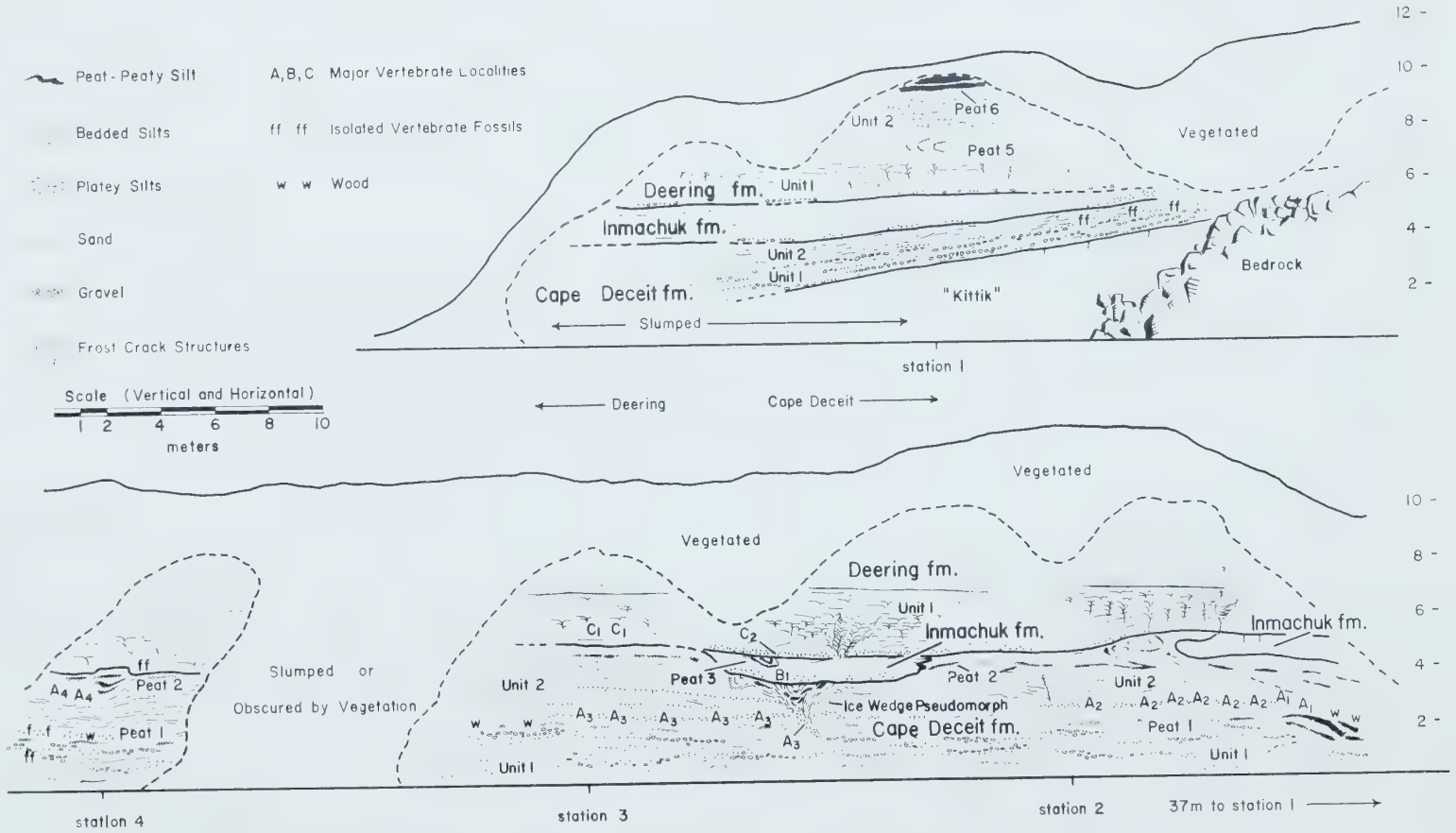
Folds in the silty, peaty facies of Unit 1 near Station 5 (Fig. 3); inclusion in the unit of gravels more angular than the locally derived beach gravels; and the banded character of the interbedded silts, sands, and gravels near Station 1 all imply that solifluction was the primary mode of deposition.

Peat 1. This unit varies from a massive, fibrous peat up to 20 cm in thickness to a thin, felted peat, or laterally intermittent zones of organic, peaty silt. Near Station 6 (Fig. 3) it begins to dip slightly, a trend which would result in its being well below the present beach level at Station 8. Peat 1 is largely devoid of tree macrofossils and large wood fragments; hence, it can hardly be a forest bed. But unpublished work in progress by one of us (Matthews) does indicate that *Larix* trees were sparsely distributed in the Deering region when Peat 1 formed.

Unit 2. Small fragments of wood 1–2 cm in diameter are common at the base of this unit which otherwise consists predominantly of nonwoody, organic, rebedded loess. Large concentrations of wood, including stumps representing trees up to 25 cm in diameter, occur immediately above Peat 1 in the basal portions of Unit 2 between Stations 4 and 6. None of the stumps are in growth position, however, and most of the wood is debarked; hence, these woody zones probably do not represent primary, buried forest beds. Instead, most of the wood in these zones is probably allochthonous, having reached its present position stratigraphically above Peat 1 by postmortal redeposition from nearby areas of higher elevation. The implication of this is that much much of the wood at the base of Unit 2 may be of the same age as underlying Peat 1, therefore, the woody zones and Peat 1 do not represent separate regional climatic events.

Between Stations 2 and 5, Unit 2 consists predominantly of grayish-olive, organic, bedded silts (reworked loess) containing a few laterally continuous thin zones of fine sand. The only evidence for solifluction in Unit 2 is restricted to the upper parts of the sequence, and in a later section this is shown to have resulted from a phase of solifluction occurring during or after the deposition of the overlying Inmachuk Formation. Thus, most of the silts in Unit 2 were probably deposited by minor episodic intervals of snow meltwater and precipitation runoff rather than by mass movement associated with solifluction. Much of the organic matter—seeds, other plant fragments, insect fragments—incorporated in the grayish-olive silts is concentrated along the bedding planes.

Near Station 5 the evenly bedded, organic silts are replaced abruptly by a sequence of massive to indistinctly bedded, inorganic, fetid, blue-gray silts. In this same area Peat 2 is deformed by slumping and subsidence while Peat 1 is sharply folded and interrupted. The coincidence of these features and the distinctive character of the silts in this area may be related to the former development and subsequent thaw of a large ice wedge. More definite evidence of ice wedges in Unit 2 of the Cape Deceit Formation is provided by an ice wedge pseudomorph located between Stations 2 and 3 (Fig. 2). This feature shows that the silts of Unit 2 were deposited in a periglacial climate which was followed by a period of thaw of sufficient duration and/or warmth to melt the ice in the ice wedge and form the sediment pseudormorph. Of added significance is the fact that the sediments of the pseudo-



FIGS. 2 and 3. Stratigraphy of the Cape Deceit Fossil Locality. Note that vertical and horizontal scales are the same.

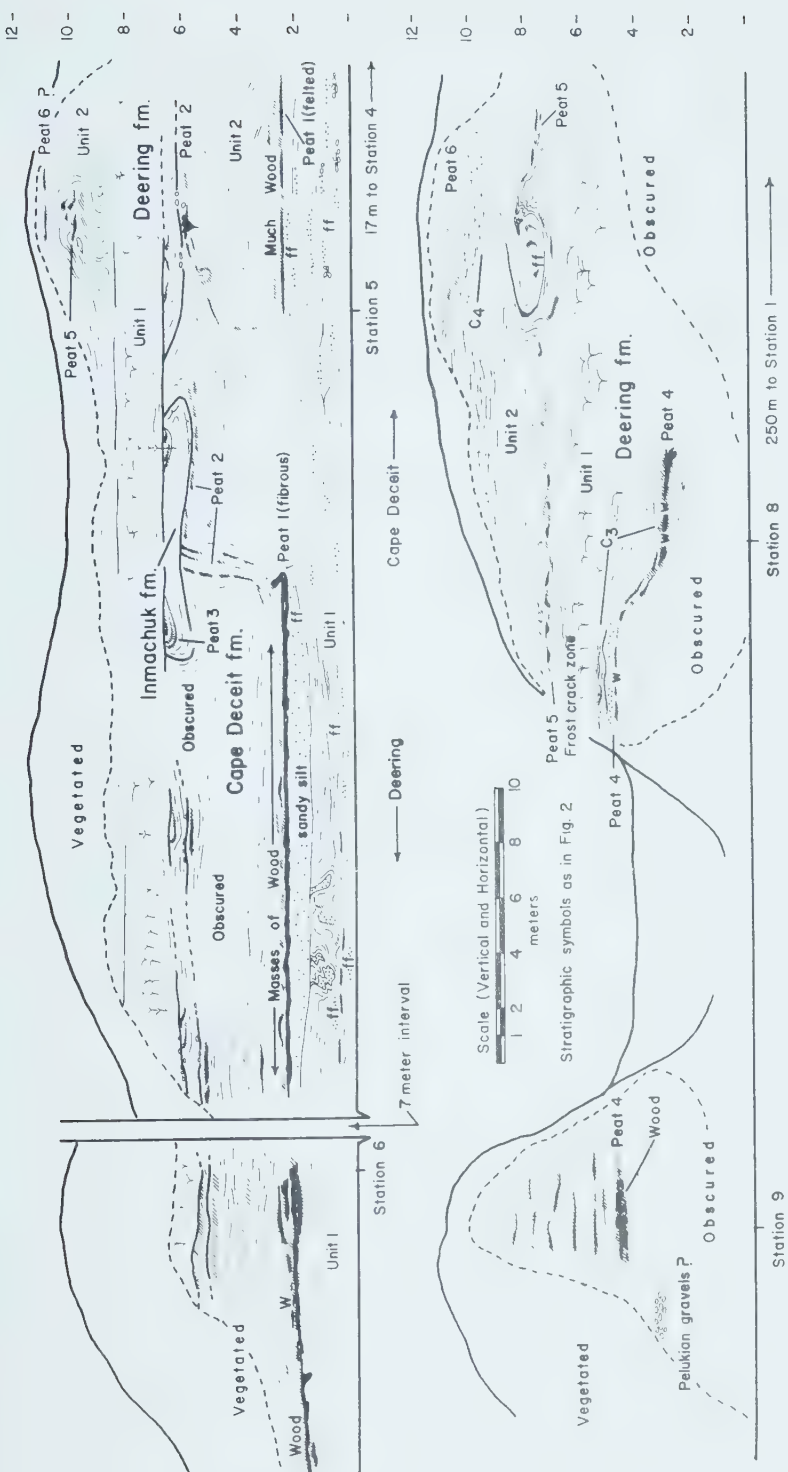

Vegetated
Wood
Unit 1
Station 6
Vegetated
Peat 5
Unit 2
Deering fm.
Unit 1
Peat 2
Peat 6 P
Inmachuk fm.
Obscured
Peat 3
Peat 2
Obscured
Cape Deceit fm.
Masses of Wood
sandy silt
Peat 1 (fibrous)
Unit 1
Much Wood
Peat 1 (felted)
Unit 2
Station 5
17 m to Station 4
Cape Deceit
Deering
7 meter interval
Scale (Vertical and Horizontal)
1 2 4 6 8 10
meters
Stratigraphic symbols as in Fig. 2
Peat 5
Frost crack zone
Peat 4
Wood
Pelukian gravels P
Obscured
Station 9
Peat 6
Unit 2
C4
Peat 5
Unit 1
C3
Deering fm.
Peat 4
Obscured
Station 8
250 m to Station 1

Figure 3

morph are in angularly uncomformable contact with sediments of the overlying Inmachuk Formation. Thus, the pseudormorph has been truncated during a period of erosion after the period of thaw responsible for its formation. Accordingly, the hiatus between the Cape Deceit Formation and the Inmachuk Formation represents a significant period of time.

Another type of periglacial feature occuring rarely in Unit 2 consists of sharply delimited blocks of silt the bedding of which is commonly rotated with respect to that of the enclosing sediments (Westgate, 1969; Dylik, 1969 for similar large-scale features). It is improbable that such features would have formed unless blocks were frozen when deposited; thus, they, like ice wedge pseudomorphs, imply the former existence of permafrost.

Vertebrate fossils of the Cape Deceit Local Fauna occur in both Units 1 and 2. In Unit 1 they are restricted to the sand and silt facies, being especially abundant in small sand lenses. Mammalian fossils occur at all levels of Unit 2; however, concentrations seem to be associated primarily with the laterally extensive, thin sand beds interbedded with the silts (localities A_1, A_2, A_3 in Fig. 2). Undoubtedly the abundance of fossils in both units is a result of secondary concentration, but good preservation of the fossils signifies that they represent an autochthonous, contemporaneous fauna. Almost all of the large mammal fossils in the fauna come from Unit 1, probably because of the greater competency of mass movement due to solifluction for transporting large bone fragments and teeth.

Inmachuk Formation

Isolated exposures of this formation occur above the contact with the Cape Deceit Formation between Stations 1 and 6. It consists of a relatively thin (1–2 meters) sequence of oxidized sands and indistinctly stratified, buff to brown, rebedded loess with a deformed and truncated zone of peaty silts (Peat 3) near the contact with overlying Deering Formation sediments. The Inmachuk Formation is distinguished from Cape Deceit Formation by features mentioned in the description of that unit. It is distinguished from the lower parts of the Deering Formation by its more organic, less sandy silts. There is little color distinction between these two formations at their mutual contact.

Both the upper and lower limits of the Inmachuk Formation are marked by laterally extensive, angular unconformities, but at some exposures, notably those near Stations 5 and 2 (Fig. 2, Fig. 3) solifluction caused structures in the Inmachuk Formation are conformable with similar structures in Peat 2 and silts of the uppermost Cape Deceit Formation. This fact indicates that the structures in both units formed simultaneously, that is, during an episode of solifluction late in the deposition of the Inmachuk Formation, but before initial deposition of the Deering Formation. Slightly more than a meter thickness of sediments were mobilized by this phase of solifluction. In order for this to have occurred the active layer, assuming the region possessed permafrost, must have been at least as thick. The current thickness of the active layer at the top of exposures is approximately one meter.

Vertebrate fossils are rare in the Inmachuk Formation (localities B_1, B_2), but one, representing the genus *Pliomys,* provides information on the probable age of the Inmachuk Formation and in turn, helps to establish the minimum age for the Cape Deceit Formation, especially when stratigraphy is also considered. This is discussed in a later section.

Deering Formation

This unit occupies the upper 3–4 meters of the exposures between Stations 1 and 6 and all of the Station 8 exposure. It is com-

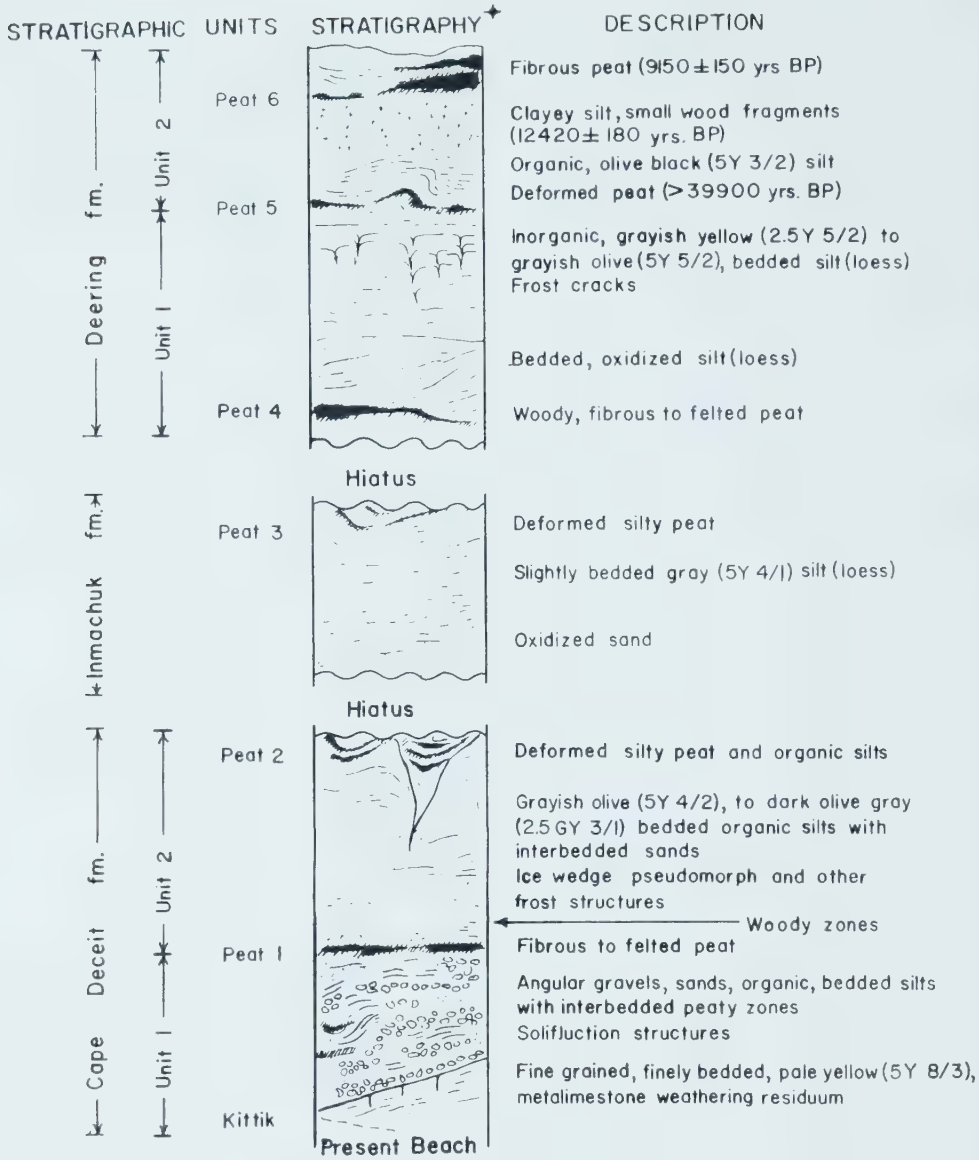
prised chiefly of inorganic, bedded loess and organic, rebedded loess. Several peat horizons are present. At some stations the basal sediments are sandy. This and the presence of bedded loess containing a pronounced zone of small wedge-shaped structures distinguishes this formation from the two other formations at the Cape Deceit exposure. Several minor stratigraphic units are present within the Deering Formation. These are:

Peat 4. Like Peat 1 in the Cape Deceit Formation, this peat is characterized by facies changes. At Station 9 it is a fibrous, woody peat more than 20 cm in thickness. At Station 8, the only other exposure of the unit, it consists of a zone of multiple, thin (2–3 cm), woody peat bands interbedded with gray sands possessing indistinct cryoturbation structures. At Station 8, Peat 4 is a forestbed containing tree stumps, wood fragments possessing bark, and spruce macrofossils (cones, needles). Initial results of pollen analysis (John V. Matthews, unpublished manuscript) plus the presence in the massive, fibrous facies of fossils of carpenter ants (*Camponotus* sp.) provides additional confirmation of this fact.

Unit 1. Occurring immediately above Peat 4 and the unconformity between the Deering and Inmachuk Formations, this sequence of sediments consists mostly of bedded, inorganic, grayish primary loess. A marker horizon composed of a laterally extensive zone of small closely spaced wedge-shaped features occurs within Unit 1 and provides the best evidence for correlation of the exposure at Station 8 with exposures nearer Cape Deceit (Figs. 2 and 3). Because of their small size, we consider these features to be frost cracks. Larger wedge shaped features, superficially similar to ice wedge pseudomorphs, also occur in the "frost crack" zone. But these larger wedges are filled with horizontally bedded, "frost cracked" silts unlike typical ice wedge pseudomorphs. Instead, they probably represent penecontemporaneously filled loess gullies (Dylik, 1966). As such they are evidence of erosion but there are no other accompanying features (i.e., weathering profiles, peats, etc.) indicating that the frost crack zone represents a significant hiatus or even a period of reduced loess deposition. In fact, at some exposures, the "frost cracks" appear to have been syngenetic (Formed during continuing loess deposition). Thus, even though the "frost crack zone" is a significant feature of Unit 1, it might have formed during a short period of time as a result of anomalous weather conditions—snowfall, winter snow drift—rather than a major climatic fluctuation.

At Station 8 and in the area between Stations 2 and 3 the basal portion of Unit 1 consists of a relatively thin sequence of sands and bedded, oxidized organic silts (Fig. 4) which, in some places are in angularly unconformable contact with overlying grayish, "frost-cracked" loess. This basal subunit contained fossils of the lemming *Dicrostonyx henseli* (localities C_2, C_3, Fig. 2, Fig. 3) providing significant evidence for the age of the Deering formation. A single fossil referred to *Dicrostonyx torquatus* occurred within the "frost crack zone" (locality C_1, Fig. 2) in the grayish primary loess which makes up the bulk of Unit 1. It is necessary for the sake of the argument presented later to emphasize that (1) this fossil came from a level stratigraphically above the intermittently exposed organic silts—*Dicrostonyx henseli* zone, (2) that the *henseli* zone occurs immediately above Peat 4 at Station 8.

Peat 5. Immediately above the grayish loess of Unit 1 is a sequence of dark organic silts (Unit 2) which contains this silty peat at its base. The best exposure of the peat occurs at Station 8 (Fig. 3) where it is seen to grade from a laterally continuous, silty facies which has been deformed by solifluction to a zone of intermittent fibrous peat nodules. Organics from several of these



✦For stratigraphic symbols and thickness of units, see Figs. 2 and 3.

FIG. 4. Idealized section showing stratigraphic units recognized at the Cape Deceit exposures.

nodules have a C-14 age greater than 39900 BP (I-4099). The lateral continuity of the nodular zone with the continuous peat facies, the fibrous character of the nodules, and their content of partially articulated beetle fossils indicate that the dated material consists neither of detrital organics or larger rebedded fragments of an older peat. Therefore, we consider the C-14 date to be an accurate indication of the minimun age of Peat 5 and the base of Unit 2.

Unit 2. The organic, olive-black peaty silts characterizing the base of this unit contrast sharply with inorganic grayish-yellow loess

of Unit 1. Like Peat 5 these silts are deformed by solifluction (Fig. 3, Station 8). At Station 8 the zone of deformation exceeds 2 m in thickness, extending in some places into the upper portions of Unit 1, and this implies at least a similar thickness for the former active zone—somewhat thicker than the present depth of seasonal thaw at Cape Deceit.

Overlying the deformed olive-black silts is a zone of horizontally bedded clayey silts distinguished by their platey structure (Figs. 2 and 3) and content of aquatic molluscs, ostracodes, and an abundance of insect fossils. Small fragments of wood interbedded with the clayey silts at locality C_4 (Fig. 3, Station 8) have a C-14 age of 12420± 180 years B.P. (I-4781). Microtine fossils were collected in association with the dated wood.

Peat 6. Above the platey silts at Station 1 is a unit of fibrous peat more than a meter in thickness (Fig. 2). Organics from the basal 5 cm of this peat have a C-14 age of 9150± 150 years B.P. (I-4780). A similar thick zone of fibrous peat occurs near the top of an exposure in a gully between Stations 6 and 8. In contrast, at Station 8 the platey–clayey silts of Unit 2 are overlain by slightly bedded silts containing only indistinct zones of fibrous peat. Occasional large wood fragments occur in the upper portions of Peat 6 at Station 1, but these are probably parts of cut and shaped logs associated with a series of Eskimo archaeologic sites located on top of the present bluffs.

Pelukian (=Sangamon) sediments. Between Deering and Station 9 isolated exposures indicate that the lower 5–6 meters of the vegetated bluffs consist of slightly weathered marine gravels capped in some places by as much as a meter of organic estuarine silts (D. M. Hopkins, personal communication, 1968). Elevation of these marine sediments and their fossils indicate that they were deposited during the Pelukian transgression (=Sangamon) (Hopkins, 1967a; McCulloch, 1967, page 106; D. M. Hopkins, personal communication, 1968) The small exposure of elevated beach gravels at Station 9 (Fig. 3) is undoubtedly of the same age; therefore, its stratigraphic relationship with Peat 4 is critical for establishing the age of the Deering formation. Unfortunately, the exposure at Station 9 did not permit an unequivocal assessment of this relationship. Peat 4 may be either (1) the terrestrial equivalent of Pelukian marine sediments (McCullogh, 1967, page 106) or alternatively (2) the Pelukian gravels may be inset in an older silt unit containing Peat 4, meaning that the approximate positional correspondence of the two units is fortuitous. In a later section we present paleontological and related evidence favoring this second alternative—that Peat 4 predates the Pelukian transgression.

It is not possible to correlate the Station 8 exposure with the portion of the Station 9 exposure overlying Peat 4, probably because Station 9 is near the former position of a Pelukian shoreline and was affected by slumping and thaw like that which occurs along the present shoreline.

MAMMALIAN SYSTEMATICS

Deering Formation

ORDER RODENTIA

FAMILY CRICETIDAE

SUBFAMILY MICROTINAE

Dicrostonyx torquatus C_4, C_1 (Figs. 2 and 3)
Dicrostonyx cf. *hensell* C_2, C_3 (Figs. 2 and 3)

Teeth referred to *Dicrostonyx hensell* from localities C_2 and C_3 at the exposure were found to span the range of variation of both *D. hensell* and the closely related, extant Nearctic species *D. hudsonius*. Most diagnostic teeth were closer to the *D. hensell* mode; hence the designation.

Occurrence of fossils of *D. hensell* at

Cape Deceit tends to support Guilday's (1963) thoughts on the evolutionary and zoogeographical implications of *D. hudsonius* which replaces *D. torquatus* on tundra east of Hudson Bay. If his hypothesis is correct, it is not surprising that Nearctic fossils of *D. henseli* include some variants of the *D. hudsonius* type.

Microtus sp. C_2, C_4 (Figs. 2 and 3)

The sample includes several M_1's but none of the diagnostic M_3's which would allow definite comparison with specimens of *Microtus deceitensis* from the Cape Deceit Formation. One of the M_1's from the Deering Formation does, however, have a more closed anterior triangle than the most complex *Microtus* M_1 variants from the Cape Deceit Formation.

Lemmus cf. *sibiricus* C_4, C_2, C_3, (Figs. 2 and 3)

Inmachuk Formation

ORDER RODENTIA

FAMILY CRICETIDAE

SUBFAMILY MICROTINAE

Pliomys sp. B_1 (Fig. 2)

Because the single M_1 is broken it is not possible to make a comparison with *Pliomys* specimens from the Cape Deceit Formation. Enough of this tooth is preserved to make the *Pliomys* designation definite.

Microtus sp. B_2 (Fig. 2)

A single M_1 is referred to this genus. A specific identification is not possible with only this single tooth.

NOTE: The small number of specimens and lack of taxonomic diversity in the Deering and Inmachuk formations (compared to the taxonomic diversity in the Cape Deceit Formation) is due to a sampling bias. Only small quantities of sediment from the Inmachuk and Deering formations were screened, the intention being to discover fossils which might contribute information on the age of the fossils from the Cape Deceit Formation.

Cape Deceit Formation

(Cape Deceit Local Fauna)

ORDER RODENTIA

FAMILY CRICETIDAE

SUBFAMILY MICROTINAE

Predicrostonyx hopkinsi gen. sp. nov.

Holotype U. A. No. 864, left mandible possessing all three lower molars (Fig. 5.). Molar lengths and widths in millimeters: M_1-, 4.4, 1.4; M_2-, 2.4, 1.3; M_3-, 2.3, 1.2.

Referred material See Table 3, Fig. 5.

Diagnosis. Distinguished from *Dicrostonyx* by the simplicity of its molar crowns. It lacks the anterior buds (nascent salient angles) on lower molars and posterior buds on upper molars. These characters occur in varying combinations in all species of *Dicrostonyx*.

Distribution. Found only in the Cape Deceit Formation at the Cape Deceit Locality.

Etymology Predicrostonyx, for its probable ancestral relationship to *Dicrostonyx; hopkinsi,* for David M. Hopkins of the U.S. Geological Survey.

Description and discussion. The earliest species of *Dicrostonyx* (*Dicrostonyx simplicior* Fejfar) comes from cave and karst fill deposits of Young-Biharian age (= Mindel) near Koneprusy, Middle Bohemia (Fejfar, 1965). Similar specimens have been reported from a site near Cologne, Germany (Heller and Brunnacker, 1966). *D. simplicior* has less complex teeth than the middle Pleistocene *Dicrostonyx henseli* (Hilton, 1926) which in turn has less complex teeth than the living *Dicrostonyx torquatus* Pallas. The *Predicrostonyx* specimens from Cape Deceit have tooth crowns much simpler than any of the previously mentioned species; hence the new generic designation.

Although the Cape Deceit specimens are markedly different from *Dicrostonyx,* there are several features which definitely relate *Predicrostonyx* to *Dicrostonyx.* (1) Both

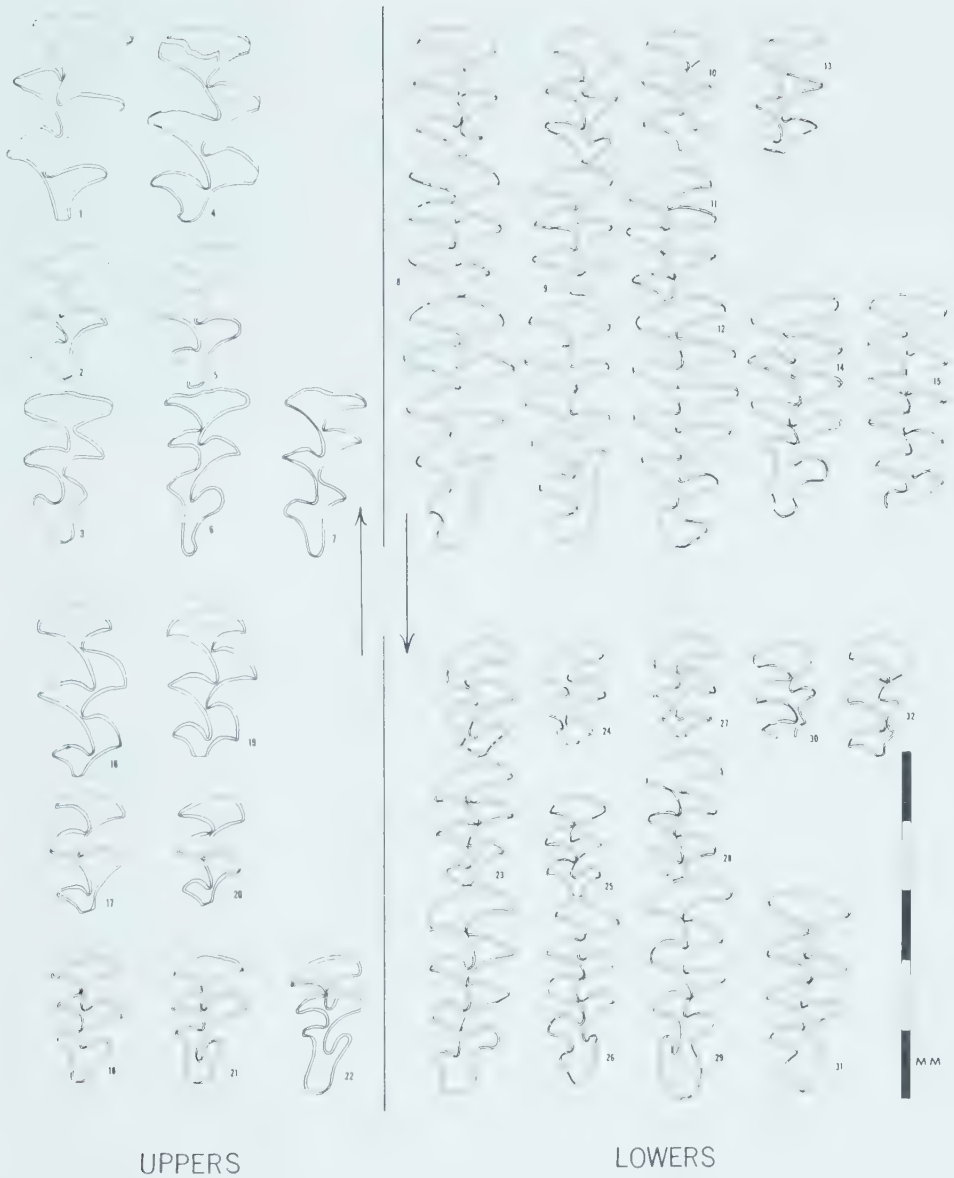


FIG. 5. Dental crown patterns of *Predicrostonyx hopkinsi* (1–15) and *Microtus deceitensis* (16–32). Holotypes: *Predicrostonyx hopkinsi*—9 (U.A. No. 864), left lower dentition (excluding incisor). *Microtus deceitensis*—23 (U.A. No. 886), right lower dentition (excluding incisor). No's. 8, 9, and 23 are complete individual tooth rows. All teeth are arranged in sequence of occurrence in mandible or maxilla (i.e., 3=M^3, 28=M_2, 31=M_1, etc.). Arrow indicates anterior direction.

genera have seven closed triangles on the M_1, a degree of complexity achieved by few other microtines. (2) All of the salient angles of *Predicrostonyx* molars are anteroposteriorly flattened and show enamel specializations, features also characteristic of *Dicrostonyx*. (3) In *Dicrostonyx* and *Predicrostonyx* the lower incisor is lingual to M_3, whereas in the superficially similar genera, *Lagurus, Microtus,* and especially *Pli-*

olemmus (which like *Predicrostonyx* has seven closed triangles in the M_1) it is labial to M_3. (4) The mandibular osteological characters of *P. hopkinsi* are similar to those of *Dicrostonyx*, i.e., the contours of the ramus are the same and the mental foramen is in an identical position in both genera.

Every molar of *Predicrostonyx hopkinsi* is distinguishable from molars of *Dicrostonyx*, though in some cases the distinctions are subtle. Following is a discussion of the variation and comparative morphology of individual teeth of *P. hopkinsi*. It should be noted at the outset that there is an overlap in variation of tooth crown morphology among species of *Dicrostonyx* (Fig. 6).

M_1. Unlike *Microtus*, the *Predicrostonyx-Dicrostonyx* lineage has undergone little evolutionary change of this tooth. There are specimens of *Predicrostonyx* which like *Dicrostonyx* have seven closed triangles in addition to anterior and posterior loops. The anterior loop of *P. hopkinsi* is, however, quite simple even compared with *D. simplicior*, the most primitive species of that

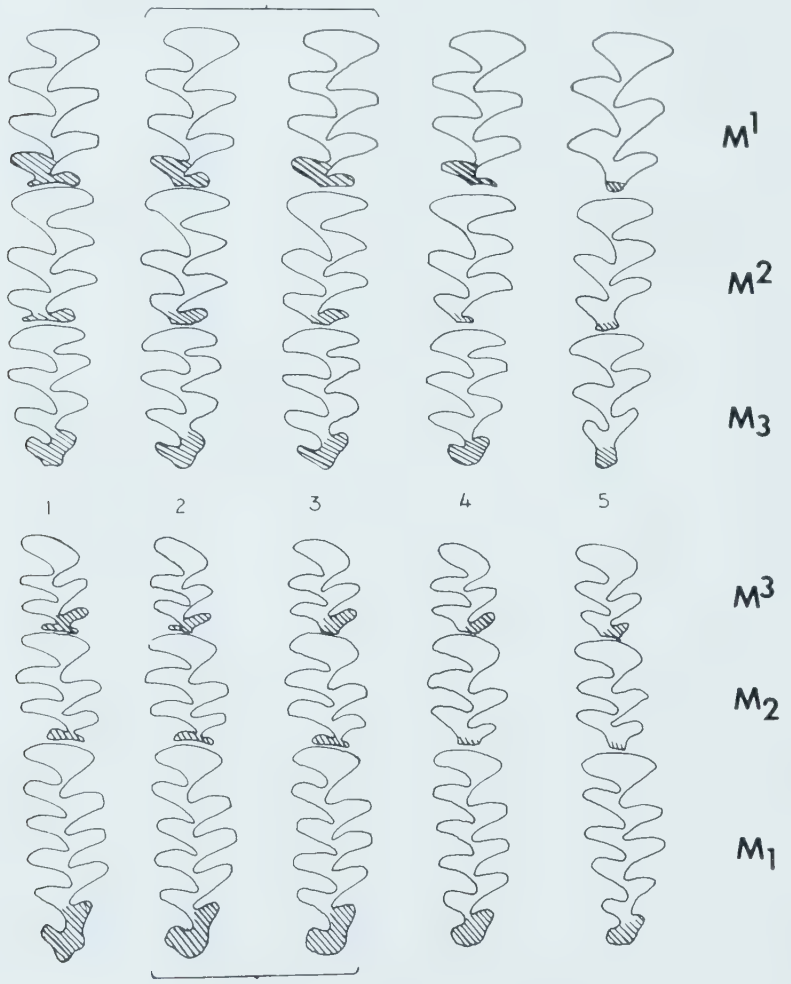


FIG. 6. Generalized molar patterns of *Predicrostonyx hopkinsi* and species of *Dicrostonyx*. 1—*D. torquatus*, 2—*D. henseli*, 3—*D. hudsonius*, 4—*D. simplicior*, and 5—*D. hopkinsi*.

genus previously known. Variation of *P. hopkinsi* M_1's is very great. Note, for example, the differences in Fig. 5. Specializations of the enamel on this tooth and others will be discussed later in this report.

M_2. In P. hopkinsi and *D. simplicior* this tooth possesses a posterior loop and four salient angles (or closed triangles). The extant species *D. torquatus* and *D. hudsonius* and the mid-Pleistocene *D. henseli* have, in addition, anterior lingual and labial buds (or angles) (Fig. 6). M_2's of *P. hopkinsi* possess no rudimentary indentations foretelling the development of these features.

M_3. The lower third molor of *Predicrostonyx hopkinsi* has a posterior loop and four salient angles. The anterior two are usually confluent to some degree. *D. henseli* possesses a lingual bud at the anterior end of this tooth and *D. torquatus* has, in addition to this, added another on the labial side. M_3's of *D. hudsonius* and *D. simplicior* resemble M_3's of *P. hopkinsi* by lacking either lingual or labial buds, but unlike these two species, many specimens of *P. hopkinsi* have only a poorly developed or rudimentary anterior salient angles (e.g., U.A. 881, Fig. 5).

M^1. In most microtine lineages this is a phylogenetically stable tooth with an anterior loop followed by four triangles, but not in the *Predicrostonyx–Dicrostonyx* lineage. The M^1's of *D. torquatus* have an anterior loop followed by six closed triangles, the last of which is incipiently developed. Attached to the sixth rounded triangle is a lingually positioned rudimentary angle or spur (Fig. 6). Possession of this feature gives *D. torquatus* the most complex M^1 of any microtine. Both *D. henseli* and *D. hudsonius* lack this small posterior lingual spur. M^1's of *D. simplicior* have a very small almost rudimentary sixth triangle or bud and the fifth triangle is more poorly developed than in other more advanced species of *Dicrostonyx*. A fifth triangle is absent in *P. hopkinsi* M^1's; however, on some teeth the fourth triangle possesses a small bud (Fig. 5–4.)—evidently the predecessor of the fifth triangle seen in *Dicrostonyx*.

Extant *Dicrostonyx* species have a comparatively small anterior loop on their M^1's. In *D. simplicior* M^1's it is larger but still smaller than the anterior loop in *P. hopkinsi* M^1's.

M^2. *D. torquatus* has an upper second molor possessing an anterior loop and five closed triangles (the fifth is bud–like in shape). Also, there is a small lingual protrusion as in the M^1. *D. hudsonius* and *D. henseli* lack this small spur. *D. simplicior* not only lacks the lingual spur, but has only a very rudimentary posterior labial bud. The M^2's of *P. hopkinsi* differ from those of *Dicrostonyx* by possessing an anterior loop and only four triangles with no evidence of a labial or lingual bud on the last of these. Moreover, the posterior two triangles in *P. hopkinsi* M^2's tend to be more confluent than in *Dicrostonyx* (Fig. 5 and 6).

M^3. The extant species of *Dicrostonyx* all have M^3's with an anterior loop followed by four triangles and a posterior lingual loop or hook. This basic pattern varies so little among the various species that even M^3's of the primitive *D. simplicior* are almost indistinguishable from those of some individual variants of extant *Dicrostonyx* species. The posterior trefoil or loop of *D. simplicior* M^3's is, however, somewhat smaller and simpler (Fig. 6).

M^3's of *P. hopkinsi* are simpler than those of *D. simplicior*. They possess only two to three closed triangles and a posterior extension which is penetrated by a re-entrant angle to form the hook normally found in species of *Dicrostonyx*. In the *Predicrostonyx–Dicrostonyx* lineage M^3's do not seem to have undergone as much morphological change as the M^1's (see Fig. 6).

Comparisons of the enamel specialization in *Dicrostonyx* are somewhat equivocal because of the great intraspecific variation of this character (Ognev, 1948). In general,

Dicrostonyx species have highly specialized enamel in which the outer crests of the salient angles lack enamel. *P. hopkinsi* has incipient enamel specializations of the same type. For example, a thin tract of enamel is missing from the pointed crests of most, but not all, salient angles; however, this character is probably subject to as much intraspecific variation as it is in *Dicrostonyx*.

Another basis for contrast of *Predicrostonyx* and *Dicrostonyx* is the shape, position, and symmetry of the angles of the teeth. The re-entrant angles of *P. hopkinsi* molars are not so narrow as those in *Dicrostonyx*, nor are the bisectors of the salient angles as nearly normal to the axis of the tooth row. Species of *Dicrostonyx* have moderately symmetrical angles; those of *P. hopkinsi* are somewhat asymmetrical.

P. hopkinsi may be considered to be ancestral to *Discrostonyx* unless it is an evolutionary relict. The latter possibility seems unlikely in view of the fact that *P. hopkinsi* possesses no dental specializations which preclude its being in the *Dicrostonyx* ancestry, and, as we mentioned above, it possesses many incipient dental features which are emphasized in *Dicrostonyx*. Thus, we conclude that although the possibility of a long-surviving ancestral form exists, it seems more probable that *P. hopkinsi* predates all species of *Dicrostonyx*.

It becomes apparent, then, that the *Predicrostonyx–Dicrostonyx* lineage was characterized by a rapid evolution of complex teeth. Unlike the *Microtus* pattern (discussed below) where some of the teeth become less complex while others increase in complexity, the *Predicrostonyx–Dicrostonyx* lineage shows an increase in the complexity of every tooth. Also, unlike the *Microtus* lineage the M_1 in the *Predicrostonyx–Dicrostonyx* lineage achieves a high degree of complexity at an early date, implying more rapid evolution than in the other teeth. The main changes of the dentition of *Dicrostonyx* after the middle Pleistocene involve increases in the complexity of the M^1 and M^3 and the addition of lingual and labial triangles to the M_3, M_2, and the M^2.

Microtus deceitensis sp. nov.

Holotype U.A. No. 886. Right mandible with three lower molars (Fig. 5). Molar lengths and widths in mm.: M_1 3.7, 1.5; M_2 2.6, 1.4; M_3 2.1, 1.1.

Referred material See Table 3.

Diagnosis. These teeth have all the characteristics of the genus *Microtus*. The molars are all prismatic and continuously growing, with cement in the re-entrant angles. The M_3 crosses to the lingual side of the incisor root. It is distinguished from other species of *Microtus* by simplicity of molar crown pattern—M^3 with two closed triangles, M_1 never with more than four closed triangles, and M_3 with second loop bisected by the posterior labial re-entrant angle.

Distribution. Found only in the Cape Deceit Formation at the Cape Deceit locality.

Etymology. Deceitensis for Cape Deceit, near the fossil locality.

Description and discussion. Morphologically, the teeth of *M. deceitensis* are among the most primitive thus far described; however, most of the dental features characteristic of *M. deceitensis* can be found in individual variants of the extant species of *Microtus*.

The collection consists mainly of individual teeth, but there are a few mandibles with more than one tooth. As in all other species of *Microtus* the M_3 of *M. deceitensis* crosses to the lingual side of the incisor root.

Representative teeth of *M. deceitensis* are shown in Fig. 5. The individual variation within the sample is similar to that found among living *Microtus* species, in which the M_1, M^3, and M_3 are the most variable teeth. Except for *M. pennsylvanicus* and *M. agrestis*, the M^1's, M_2's and M^2's of extinct and extant species do not exhibit a great de-

gree of interspecific variation. These teeth in *M. deceitensis* differ little from those in extant *Microtus* species.

M_3. The second lingual loop tends to be bisected by the posterior-labial re-entrant angle (Fig. 5). Among North American microtines this trait and degree of complexity is found commonly in two extant species, *M. umbrosis* and M. *guatemalensis,* both confined to mountain refugia in Central America and both probably evolutionary relicts. Significantly, no known *Microtus* lineage shows an increase in the complexity of M_3. Perhaps because of the M_3's unusual relationship to the incisor root, it alone has undergone reduction while all other teeth were evolving toward greater complexity.

M_1. The first lower molar is used more frequently than any other tooth to characterize microtine taxa. The reason for this is that it has consistently evolved more rapidly than any other tooth. All *M. deceitensis* specimens possess a posterior loop followed by four closed triangles and an anterior hook-shaped loop that generally has a rudimentary salient angle on its labial face. The degree of closure of the fourth triangle is subject to variation. Only the two *Microtus* subgenera, *Pedomys* and *Pitymys,* have fewer closed triangles, and in these it is because of their peculiar characteristic of having the fourth and fifth triangles broadly confluent. *M. deceitensis* has a simpler tooth shape. It approximates the tooth shape found in the extinct *M. paroperarius* (Paulson, 1961); however, the latter is slightly more complex than *M. deceitensis.* The *M. deceitensis* M_1 is morphologically most similar to that of the extant *M. oeconomus,* but it displays characteristics that overlap with M_1's in both this species and the previously mentioned *M. paroperarius.* The simple M_1 in *M. oeconomus* implies that it is an evolutionary relict, reflecting a morphological stage which was attained early in the history of the genus. The three species, *M. oeconomus, M. paroperarius,* and *M. deceitensis,* have a less complex M_1 than the extant *M. pennsylvanicus* which sometimes has as many as seven closed triangles to a posterior loop and trefoil.

M^3. All specimens of this tooth possessed two triangles with a posterior hook or an open triangle and hook (Fig. 5). Only the American *Microtus* subgenera *Pedomys* and *Pitymys* and a few variants within the nominal subgenus have as few closed triangles. The constant simplicity of M^3's in *M. deceitensis* shows that it is one of the most primitive *Microtus* species.

In conclusion, *M. deceitensis* is similar to fossils of *M. paroperarius* in almost every respect except that the M_3's of *M. deceitensis* are slightly more complex while its M_1's almost never have five closed triangles between the anterior loop and the posterior trefoil like M_1's of *M. paroperarius.* Thus, *M. deceitensis* is more primitive than *M. paroperarius. M. paroperarius* appears in Late Kansan time in North America, and until the discovery of the Cape Deceit locality represented the earliest Nearctic record of the genus.

The earliest Palaearctic occurrence of *Microtus* is in sediments of Gunz II age from the Cromer forest series (Kurten, 1968). Shortly thereafter, *Microtus* became a common element of European faunas (see Kurten, 1968 and Fejfar, 1961 for a review). The major theme of *Microtus* evolution in the Palaearctic has been increasing dental complexity (especially of the M_1 and M^3). With the exception of M^3's in the *M. nivalinus–M. nivaloides–M. nivalis* group, Palaearctic species of *Microtus* possess a more complex dentition than *M. deceitensis. M. raticepoides* has a comparable M_1; contemporaries (as *M. arvalinus*) have more complex M_1's. The M_3's in those species are less complex than those of *M. deceitensis,* but, as we mentioned above, this is probably a progressive rather than primitive feature. The two Chinese fossil *Microtus* species from Choukoutien are both more advanced

in complexity than *M. deceitensis*. One, *M. epiratticeps*, has a much more complex M^3 and *M. brandtioides* has a more complex M_1, other than that they are fairly similar (see Young, 1935).

Judging from tooth size, *M. deceitensis* was about the size of medium to small extant *Microtus* species. With the exception of the characteristics mentioned above, other features—the degree of angular alternation, enamel specialization, and salient angle compression—are similar in most species of *Microtus* including *M. deceitensis*.

Some of the *M. deceitensis* molars are quite similar to those of *Predicrostonyx hopkinsi*. The chief difference of taxonomic significance is the shape of the anterior and posterior surfaces of the salient angles. They are curved in *Microtus* and flattened in *P. hopkinsi*. The difference is especially obvious in a comparison of the anterior surfaces of the upper molars and the posterior surfaces of the lower molars (Fig. 5).

Pliomys deeringensis: sp. nov.

Holotype U.A. No. 861. Right mandible possessing the M_1 and M_2 (Fig. 7). Molar length and widths in mm.: M_1, 3.7, 1.5; M_2, 2.1, 1.4.

Reference material. See Table 3.

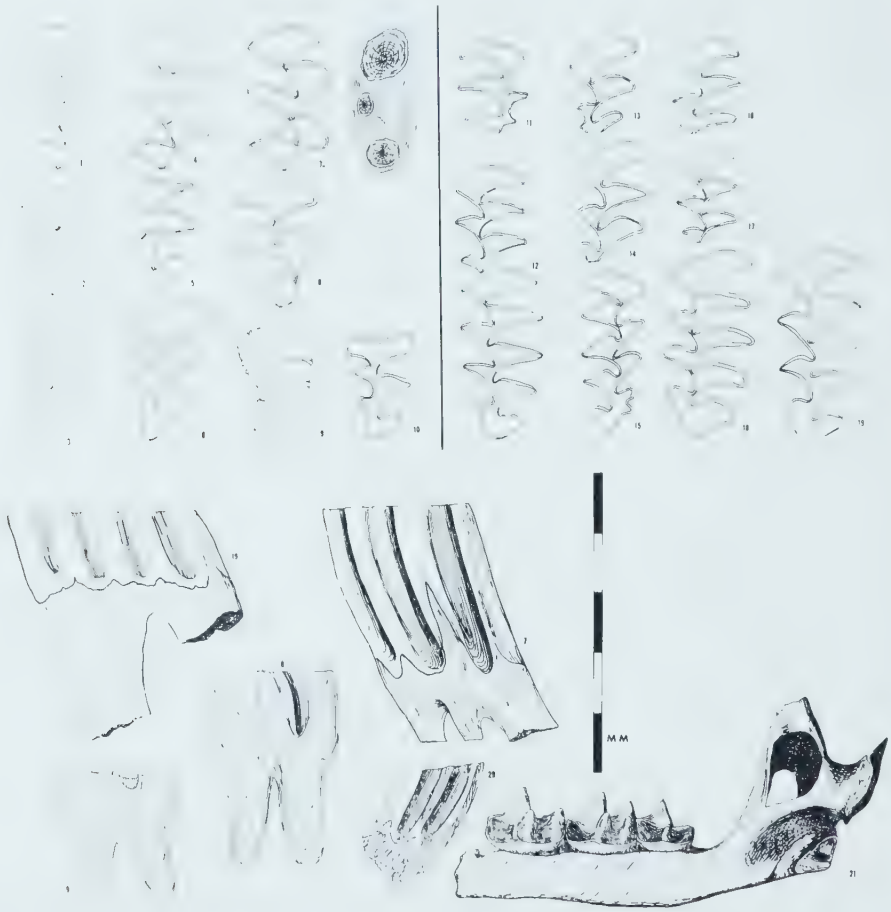


FIG. 7. *Pliomys deeringensis:* 1–20. *Sorex* (*Sorex*) sp.: 21. Holotype: *Pliomys deeringensis*—12 (U.A. No. 861), right M_1–M_2. Note ontogenetic as well as interindividual variation of *Pliomys* M^3's (3, 6, 9, and 10). Uppers 1–10, Lowers 11–19.

Diagnosis. Distinguished from other *Pliomys* species by its greater dental simplicity. Dentine tracts on crests of salient angles are poorly developed or absent.

Distribution. Found only at the Cape Deceit locality.

Etymology. Deeringensis from Deering, the Eskimo village near the fossil locality.

Description and discussion. The genus *Pliomys* occurs commonly in fossil assemblages of early and middle Pleistocene age in Eurasia. *Pliophenacomys,* a late Pliocene genus from western United States bears some resemblance to *Pliomys,* but as Hibbard pointed out (1959), there are distinct differences. Hibbard feels that *Pliomys episcopalis* is closely related to the genus *Microtus,* or at least to the stock that gave rise to *Microtus.* These similarities are well-illustrated in the Cape Deceit Local Fauna by *Pliomys deeringensis* and *Microtus deceitensis,* but if they are related, the occurrence of both genera in that assemblage shows that their common ancestor must be order than the Cape Deceit formation. Another interpretation of the ancestry of *Microtus* is that it is derived from *Allophaiomys pliocaenicus* Kormos (Chaline, 1966).

Although some consider *Pliomys* to be synonomous with *Dolomys,* it does not seem reasonable in view of the differing trends in the radiations of the two genera. Another puzzling categorization by European paleontologists is the separation of *P. episcopalis* and *P. lenki* on the basis of subtle differences in the shape of the trefoil of the M_1, even though both variants and intermediates are found in the same deposits (Fejfar, 1965). *P. lenki* is the more complex of the two. The dentition of *P. deeringensis* is as variable as that in both of these European species, but on the average much less complex. Also, specialization of enamel thickness and the lack of enamel interruptions on the crests of the loops and salient angles is not so well-developed in *P. deeringensis* as it is in *P. episcopalis* and *P. lenki.* For example, both of the latter species have interrupted enamel surfaces on the lingual and labial sides of M_1, with some tendency for interruptions to occur in other areas. Although the enamel is quite thin at comparable sites on *P. deeringensis* molars, it is rarely completely removed. (U.A. 101, Fig. 7 is one of the exceptions). Some abraded teeth have enamel interruptions, but it is difficult to tell whether these are natural or result from sieving (U.A. 1167, Fig. 7). Since *Pliomys* teeth are not prismatic, intraspecific variation in occlusual patterns is compounded by ontogenetic variation.

M_1. The first lower molor of *P. deeringensis* consists of a posterior loop with five closed triangles and a rather simple anterior lobe. The mean complexity of this lobe or hook is less than in M_1's of the *P. episcopalis–P. lenki* complex; however, individual variants are similar to *P. episcopalis.* Only rarely does the posterior loop of *P. deeringensis* lack enamel at the angles, a character that is seemingly universal for *P. episcopalis* and *P. lenki.*

All other teeth of *P. deeringensis* appear to be similar to other species of *Pliomys;* however, European taxonomists have failed to emphasize or figure upper molars, consequently preventing comparisons with the uppers of *P. deeringensis.* None of the teeth of *P. deeringensis* have cement in the re-entrant angles. There is size overlap between *P. deeringensis* and the *P. episcopalis–P. lenki* group in every tooth, including the M_1. Three roots are formed by M^1; the other teeth have two.

We feel the differences between *P. deeringensis* and other *Pliomys* species as well as the geographical range extension of the genus that the Cape Deceit find represents, warrants the new specific designation.

If a future revision of the genus shows that many of the established *Pliomys* species are variants of one extremely variable species, then *P. deeringensis* may have to be considered an intraspecific variant rather

than a distinct species. In any event, *Pliomys deeringensis* is, in general, morphologically more primitive than the Palaearctic species *P. episcopalis* and *P. lenki.*

Lemmus cf. *sibericus*

Referred material. See Table 3.

Remarks. No difference in crown pattern, distribution of enamel, or size could be found between the Cape Deceit *Lemmus* and extant representatives of the genus. Only teeth and mandibles were examined, as in the case of the other species, though other skeletal elements were collected. Rausch (1953) synonomized the Alaskan *Lemmus* species with the Siberian *Lemmus sibericus.* The Cape Deceit *Lemmus* fossils are tentatively referred to this species; however, it should be emphasized that the teeth of *Lemmus lemmus, Lemmus sibericus,* and members of the genus *Myopus* show overlap in almost every dental character related to shape.

It is peculiar that *Lemmus* should have reached its present complexity so early in the Pleistocene (see Table 1), for it is one of the most specialized microtines in modern small mammal communities. Pitelka (1957) found that *Lemmus* is the most abundant microtine on the Northern Coastal Plain near Barrow, Alaska; and Thompson (1955) noted that they occupy a very specific type of habitat—wet areas with polygonal ground microrelief. They feed primarily on the vegetative parts of sedges and grasses. Since there has been no apparent change in the dentition of *Lemmus* during the middle and late *Pleistocene,* it is possible that its food and habitat requirements have also remained unchanged.

Family Sciuridae

Marmota sp.

Referred material. Individual molars, premolars, and incisors along with fragmentary postcranial elements.

Remarks. The material was not adequate for a specific determination. *Marmota* fossils differing only slightly from extant specimens have been found in Hemphillian (middle Pliocene) deposits in Nevada. Repenning (1967) states that *Marmota* immigrated to Asia during the late Pliocene (Csarnotan), but did not reach Europe until mid-Pleistocene (Elster I).

Citellus (=*Spermophilus*) sp.

Referred material. Individual molars, premolars, incisors, and postcranial fragments.

Remarks. The teeth appear to be very similar to the extant species *Citellus parryi* which occurs across Siberia, Alaska, and the Yukon Territory. *Citellus* teeth have been found in the Fairbanks area of interior Alaska in sediments thought to be of Illinoian age (Guthrie, 1968a). Repenning (1967) reviews the despersal of *Citellus* to the Palaearctic. It first occurs in Europe during the Gunz glaciation and in China during the middle Pleistocene.

Order Lagomorpha
Family Ochotonidae

Ochotona whartoni sp. nov.

Holotype. U.A. No. 2000. Mandible with two molars (Fig. 9). Length of molar row from P_3 to M_2: 9.7 mm. Width of M_1: 2.8 mm.

Referred material. Jaw fragments, incomplete individual molars, and two complete maxillary tooth rows from different individuals, all from Cape Deceit; and a comparatively complete skull with mandibles from the Gold Hill Cut, Fairbanks (American Museum of Natural History, uncataloged specimen; O. Geist no 4516).

Diagnosis. The fossils are well out of the size range of any known living species of *Ochotona,* yet the teeth are of the typical *Ochotona* type. The large size of the Cape Deceit specimens is the chief justification for their being assigned to a new species. The Gold Hill specimen is somewhat

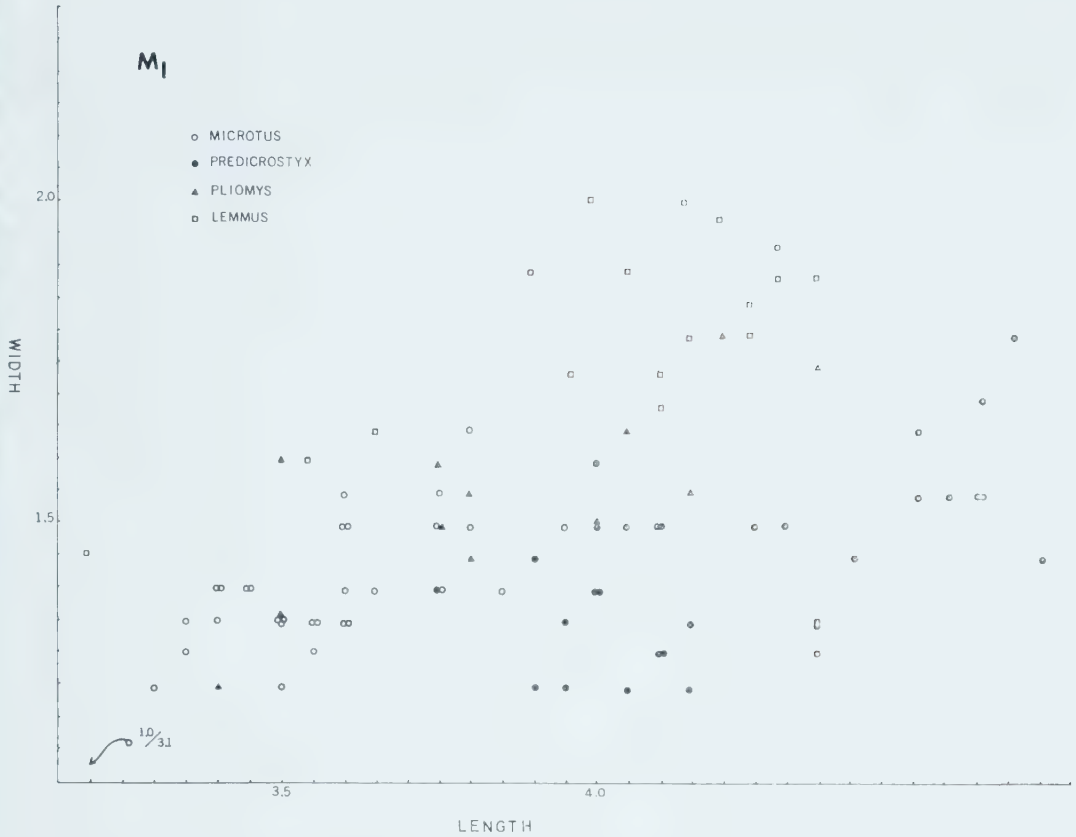


FIG. 8. Scatter diagrams in millimeters of lengths and widths of measurable teeth of *M. deceitensis, P. hopkinsi, P. deeringensis,* and *Lemmus* of *sibericus* from Cape Deceit Local Fauna.

smaller than the Cape Deceit specimens, but not enough to warrant a separate specific designation.

Distribution. Cape Deceit locality and the Gold Hill mining cut 11 km west of Fairbanks, Alaska.

Etymology. Whartoni after the late George B. Wharton who helped in the initial collecting at Cape Deceit.

Description and discussion. The rami and maxillary tooth rows from Cape Deceit are somewhat larger than the Gold Hill specimens. Both differ only in size from modern ochotonids. The Gold Hill specimen was in a very hard matrix. It was found in 1954 as part of a concretion on the upper surface of the gold-bearing gravels. Other fossils found in similar concretions from the same level represent *Citellus undulatus* and *Microtus miurus.* The smaller size of the Gold Hill specimen and its occurrence with *M. gregalis,* the earliest records of which are definitely younger than the Cape Deceit Local Fauna, suggests that there is a temporal separation between the Cape Deceit and Gold Hill specimens, possibly explaining the size difference.

Ochotona teeth seem to vary little from species to species. In contrast with the leporids, the ochotonids have undergone little radiation since their first appearance in the Pliocene of North America. Both the earliest North American species and the extant North American species are comparatively small sized; however, larger extant species exist in Eurasia (Ognev, 1940). Still, *O.*

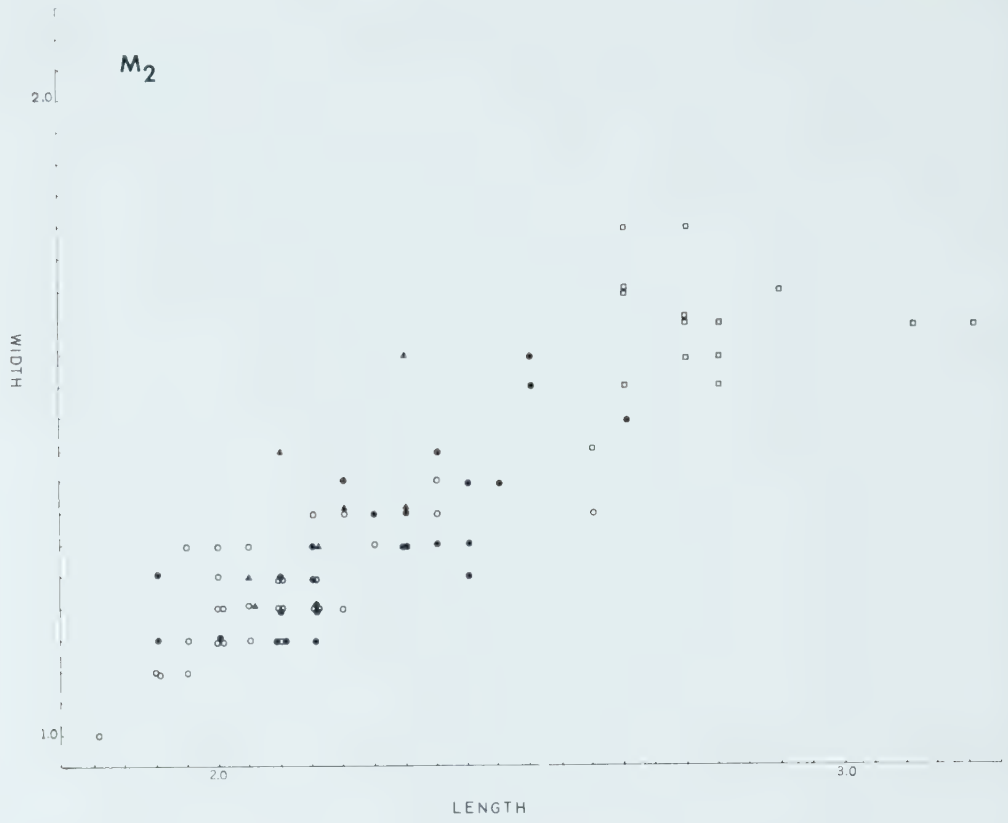


Figure 8—Continued

whartoni is considerably larger than any extant species, suggesting either that it was a phylogenetic side branch that later became extinct or that present ochotonids (the northern ones at least) went through a period of large size in their evolutionary history. There are several fossil species of size similar to *Ochotona whartoni* found in Pleistocene deposits of China. For example, *Ochotona koslowi* Buchner has a tooth row averaging around 8.5 mm, and *Ochotona complicidens* Tielard and Young has a tooth row over 12 mm (Young, 1935). The latter is early Pleistocene (Nihowan) in age and the former is from the Choukoutien beds, now thought to be chronologically near to late Mindel age. It appears that *O. whartoni* is closely related to these species as it falls between them in its only diagnostic character —size. We chose to list it as a separate species at this time because of the great geographic distance between it and the other related members and the general lack of detailed osteological information—however, we wish to emphasize the similarities and the potentially close relationships.

Order Insectivora
Family Soricidae

Sorex (Sorex) sp.

Material. Two lower mandibles with the anterior parts missing.

Remarks. The specimens are not sufficient for a specific determination, but the condyle shape (Fig. 7) and position of the mental foramen indicate that they are from *Sorex*. The lack of a postmandibular canal indicates that the specimens belong to the subgenus *Sorex*.

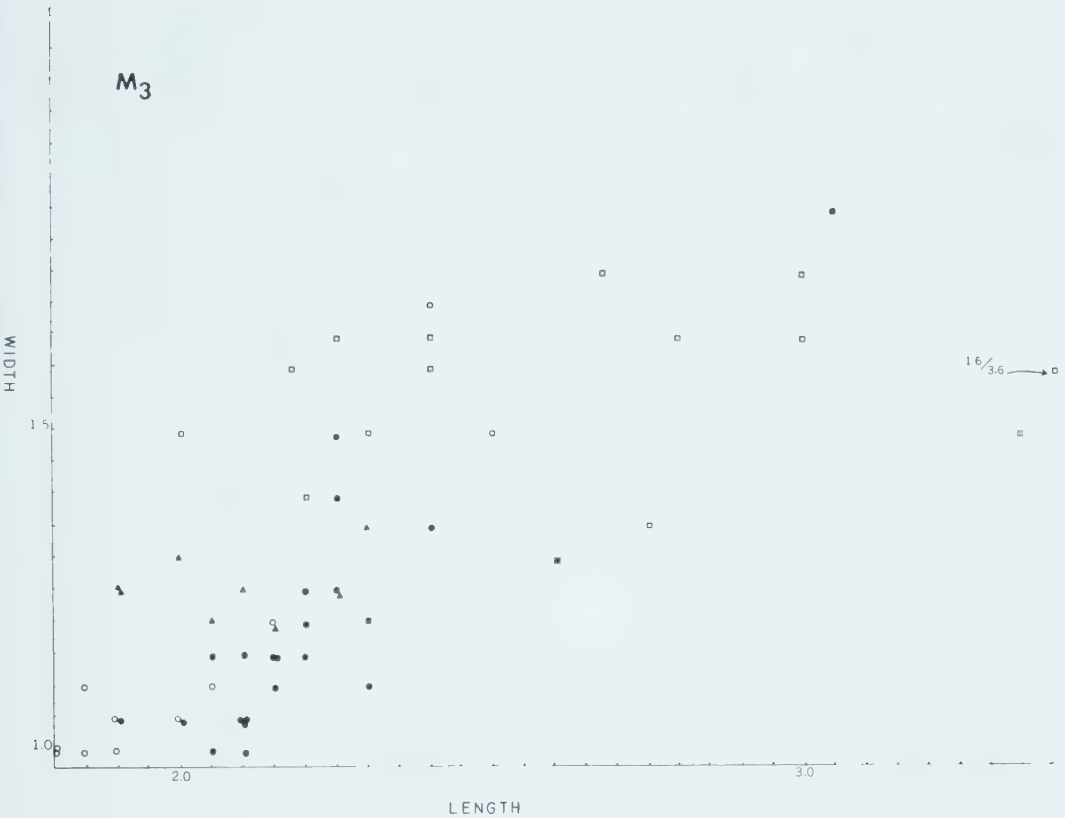


Figure 8—Continued

Order Perissodactyla
Family Equidae

Equus sp.

Material. One unerupted deciduous premolar (Fig. 10[3]), a worn specifically indeterminate molar, a third and two first phalanges, a partial pelvic girdle, and a fragmented radius.

Remarks. Since *Equus* is thought to have migrated to the Nearctic at the beginning of the Irvingtonian Land Mammal age (middle Pleistocene), *Equus* fossils of probable pre-Mindel age are not unexpected at a site such as Cape Deceit (Table 1). It is unfortunate that more material is not available since, if our assessment of the age of the site is correct (see Table 1), it represents a time when both zebrine and cabaline horses existed in Eurasia. Sher (1969), for example, records a *stenonis*-like (zebrine) horse from the early to middle Pleistocene Olyor deposits in northeastern Siberia. Unfortunately, none of the Cape Deceit fossils can be assigned to species.

The third phalange (Fig. 10) is larger than most of those that were collected from deposits of Illinoian and Wisconsin age in the Fairbanks area in interior Alaska.

Order Artiodactyla
Family Cervidae

Cervus cf. *elaphus*

Material. A cuboid-navicular and a P^4 from a medium-large-sized cervid (Fig. 10).

Remarks. The cuboid-navicular is too small to belong to *Alces* and to large for *Rangifer*. It fits quite well with *Cervus ela-*

[3] The unerupted premolar was sectioned in the hopes that more precise identification could be made than generic status.

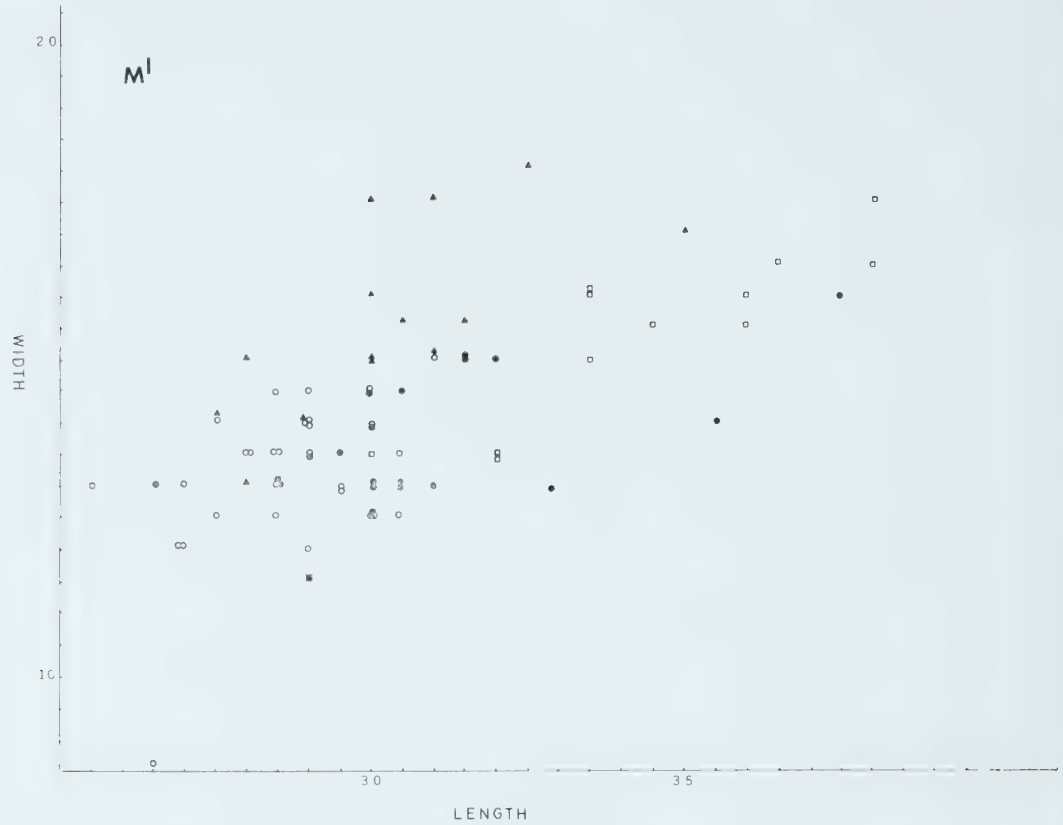


Figure 8—Continued

phus specimens from North America. In a previous study (Guthrie, 1967) *Cervus* was shown to be a moderately common element in the Wisconsin and Illinoian large-mammal communities in Alaska. This specimen extends the history of *Cervus* in the Beringian area to pre-Illinoian times (Table 1).

Rangifer sp.

Material. A DP^{3}, moderately well-worn (Fig. 10).

Remarks. Péwé and Hopkins (1967) reported *Rangifer* from Illinoian deposits in Alaska, until that time the earliest North American record of the genus. It appears as early as Gunz II in Europe (Kurten, 1968). The rarity of fossils of this genus in early Pleistocene contexts may be because its evolution occurred predominantly in boreal and arctic environments—often poorly represented in the fossil record. In a later section we will discuss our reasons for concluding that *Rangifer* as well as other taxa of the Cape Deceit Local Fauna evolved in Holarctica. If this is so, any argument as to the continent of origin becomes academic.

Order Carnivora
Family Canidae

Canis sp.

Material. A canine tooth with the dimensions of that of the modern wolf, *Canis lupus* (fig. 10).

Remarks. The Canis identification is tentative, since a lower mandible of another canid genus, *Xenocyon* (=*Cuon*), has been found in possible pre-Illinoian sediments in the Fairbanks area (Cripple Creek Sump) (Péwé and Hopkins, 1967).

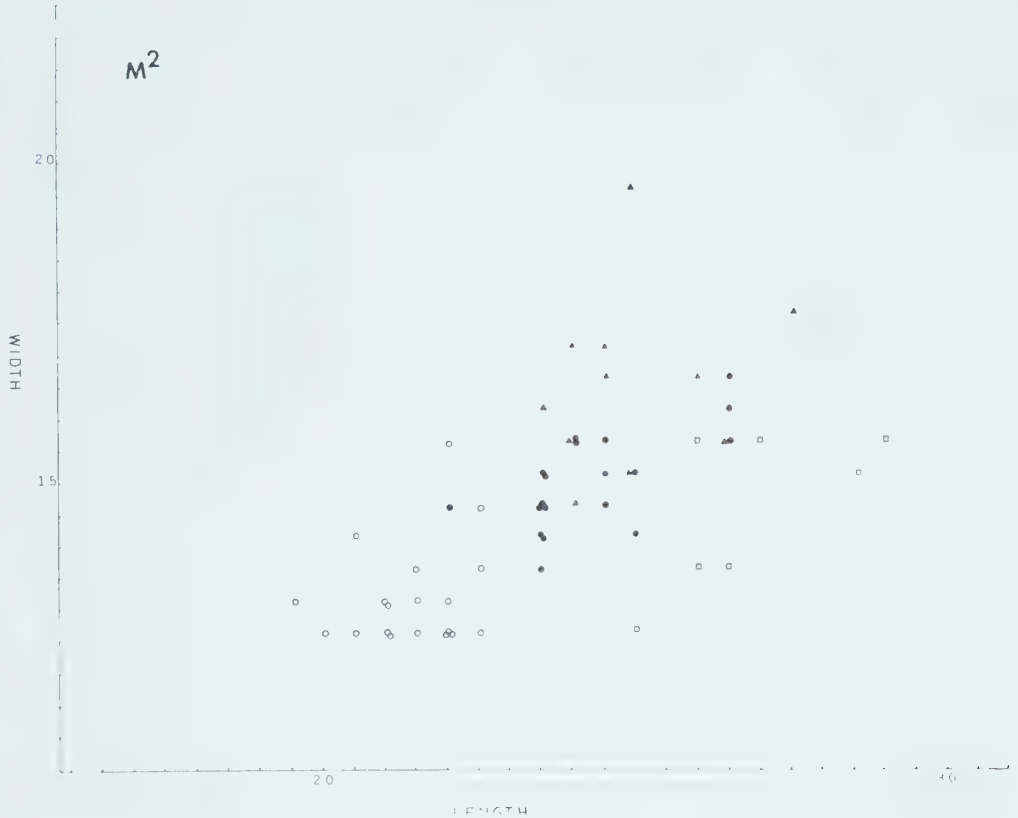


Figure 8—Continued

GEOLOGIC HISTORY AND AGE

The probable sequence of Quaternary events at Cape Deceit is presented in Table 1. A primary assumption is that loess deposition and redeposition as organic colluvium at Cape Deceit coincided with periods of glaciation elsewhere in Alaska; whereas, prominent angular unconformities, thaw features, and laterally extensive, thick peat horizons formed during interstadials or interglacials. Figure 11 shows that the most probable source for loess in the Cape Deceit exposure was outwash streams draining glaciers in the western Brooks Range. Differences in the extent of Wisconsin and Illinoian glaciers in that area, as well as the blocking effect that the Illinoian terminal moraine complex at Baldwin Peninsula (Fig. 11) would have had for Wisconsin outwash streams, explains the relative thinness of Wisconsin sediments at Cape Deceit. While there is no evidence of pre-Illinoian ice positions in the western Brooks Range area, evidence from Nome showing early Pleistocene Iron Creek drift to be nearly co-extensive with Illinoian Nome River drift (Nelson and Hopkins, 1969) Fig. 11), suggests that some pre-Illinoian glaciers in the western Brooks Range may have, like Illinoian glaciers, closely approached the Deering area. This would explain the relatively thick sequence of rebedded loess in the pre-Illinoian portions of the Cape Deceit exposure.

Paleontological evidence provides the chief criteria for dating stratigraphic units at the Cape Deceit locality. In the systematic section dealing with the Cape Deceit Local Fauna evidence is presented to show that specimens of the three microtine taxa,

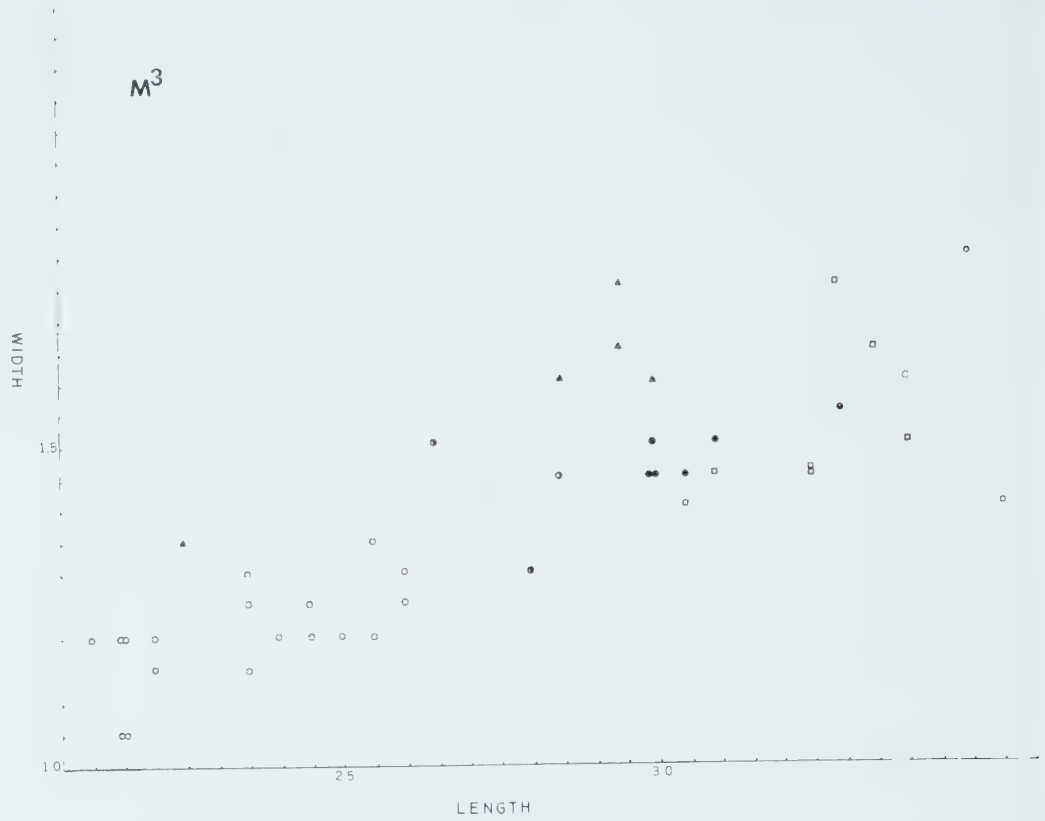


Figure 8—Continued

Predicrostonyx hopkinsi, Microtus deceitensis, and *Pliomys deeringensis* are morphologically more primitive than the earliest known related taxa of the same genera. If none of these taxa are evolutionary relicts —members of independently evolving, less progressive lineages—then this is also evidence of relative age. But such an assumption cannot be made for *Pliomys deeringensis,* for its occurrence at the Cape Deceit locality, the easternmost and only Nearcitic record of the genus, as well as the absence of *Pliomys* fossils from eastern Siberia (Vangengeim, 1961; A. Sher, private communication, 1969) suggests that *P. deeringensis* may have been just such an isolated and, therefore, independently envolving lineage. *Pliomys* became extinct in most of Europe before the Riss (penultimate) glaciation (Kurten, 1968). It has not been recorded from Riss and Würm contexts in eastern Siberia or from the Illinoian, Wisconsin of Alaska (Vangengeim, 1961; Repenning, 1967). Thus, even if *P. deeringensis* is an evolutionary relict, the sediments in which it occurs almost certainly predate the Illinoian (Riss).

There are no similar compelling reasons for assuming that either *Predicrostonyx hopkinsi* or *Microtus deceitus* are evolutionary relicts. Sediments containing *Predicrostonyx hopkinsi* probably predate the European Mindel glaciation during which the most primitive species of *Dicrostonyx* (*D. simplicior*) appeared (Fejfar, 1965).

Fossils of *Microtus deceitus* provide more definitive evidence for the age of the Cape Deceit formation. The earliest European re-

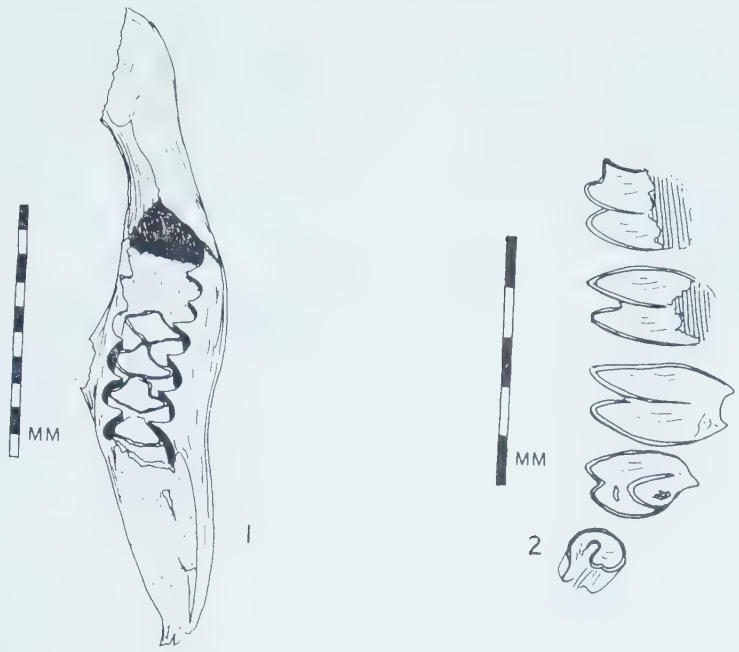


FIG. 9. *Ochotona whartoni*. Holotype: 1 (U.A. No. 2000), incomplete right mandible with M_1–M_2. 2: Right upper dentition (excluding incisors) of specimen from Gold Hill locality, Fairbanks (see text).

cord of the genus is from sediments of Gunz II age (Kurten, 1968); *Microtus paroperarius*, until this paper, the earliest known and most primitive species from the Nearctic, is part of the late Kansan Cudahy Fauna from the central United States. The more primitive *Microtus deceitensis* antedates both the earliest European and North American records of the genus, suggesting that the sediments of the Cape Deceit Formation in which it occurs predate both the European Gunz II stage and the late Kansan stage of the North American mid-continent.

This conclusion for the age of the Cape Deceit formation is not contradicted by the temporal ranges of the remainder of the Cape Deceit local fauna. For example, *Lemmus* sp., though unknown in North America before the Illinoian (Repenning, 1967), occurs as early as Gunz II in Europe (Kurten, 1968). Likewise, *Rangifer* and *Cervus elaphus* (=*Cervus acoronatus*), previously unknown in the Nearctic before middle and late Pleistocene time (Kurten, 1966), occur in earlier contexts in the Palaearctic. *Cervus elaphus* is represented in the Gunz age Sussenborn gravels of Germany (Kurten, 1968), and recently Sher (1969) has reported a *Rangifer*-like cervid from the middle Pleistocene or older Olyor silts in eastern Siberia.

The single specifically indeterminate *Pliomys* fossil from the Inmachuk Formation probably indicates, according to the information presented earlier, that those sediments were deposited in pre-Illinoian time, and occurrence of fossils of *Dicrostonyx henseli* in basal sediments of the overlying Deering Formation tends to strengthen this conclusion (see discussion below). That the Inmachuk Formation is of pre-Illinoian, pre-Riss age is some confirmation of our Gunz II assumption for the minimum age of the Cape Deceit Formation. The two formations are separated by a hiatus presumably representing an interglacial (period of thaw and erosion), which means that the Cape

FIG. 10. Large mammal fossils from the Cape Deceit Local Fauna. 1: *Equus* sp.—section of an unerupted deciduous upper premolar. 2: *Cervus?*—p^4 from a medium-size cervid. 3: *Canis* sp. ?—worn canine. 4: *Cervus* cf. *elaphus*—cuboid-navicular. 5: *Equus*—terminal phalanyx. 6: *Rangifer* sp.—DP^3.

Deceit Formation can be no younger than the Gunz stage if the Inmachuck Formation is no younger that the European Mindel stage. Remember, also, that the Cape Deceit Formation possesses evidence within itself of an interglacial or interstadial (Peat 1); therefore, parts of the formation may even predate the European Gunz II stage.

The use of European stage names (i.e., Gunz, Mindel, etc.) instead of North American terminology in references to the age of the Cape Deceit and Inmachuk Formations is awkward but unavoidable because (1) European sites contain the best documented fossil record of many of the mammalian taxa occurring at Cape Deceit and (2), because there is at present no general agreement on correlation of European and North American early and middle Pleistocene glacial sequences (see Richmond, 1965, for one interpretation and Kurten, 1963, for other alternatives). It is just as difficult to relate the Inmachuk and Cape Deceit Formations to an Alaskan Quaternary sequence. The problem is that the early and middle Pleistocene of western Alaska is represented chiefly by a series of marine (interglacial) transgressions (Hopkins, 1967a) of which there is no evidence at the Cape Deceit locality. Even so, our assessment of the age of the Cape Deceit Formation indicates that it predates the Einahnuhtan transgression, considered by Hopkins (1967a) to be the possible equivalent of the interglacial which preceded the Alpine Mindel glaciation. It may even predate or in part be correlative with the Anvilian transgression which Hopkins (1967a) believes occurred between 0.7 and 1.0 m. y. ago.

Sea levels during both the Einahnuhtan and Anvilian transgressions were probably higher than the present elevation of the Quaternary exposures at Cape Deceit (Hopkins, 1967a). It is strange, then, that

the only marine sediments in the exposures represent a late Pleistocene transgression (Pelukian). The explanation for this paradox may be that the coastal area near Deering has subsided. Such movement might have coincided with a post-Pliocene uplift of some tens of meters in the area approximately 40 km south of Deering (Hopkins *et al.,* 1971).

According to C-14 dates the upper part of the Deering Formation is of Wisconsin age. Fossils of *Dicrostonyx henseli* from the base of Unit 1 indicate that the lower portions of the formation probably predate the Wisconsin. The reasoning for this conclusion is as follows.

D. henseli, an extinct species previously known only from European localities, is closely related to the extant *D. hudsonius* which is restricted to the tundra east of Hundson Bay. Guilday (1963) hypothesized, correctly it now seems in view of the Cape Deceit *D. henseli* record, that the subgenus in which both *D. henseli* and *D. hudsonius* are placed once had a much wider distribution in Asia and North America before being replaced in all areas except east of Hudson Bay by the more complex toothed species, *D torquatus.*

Dicrostonyx torquatus is the only species of the genus to be found in Illinoian and Wisconsin sediments in Alaska (Guthrie, 1968a; Repenning *et al.,* 1964). It has even been reported from pre-Illinoian contexts (Péwé and Hopkins, 1967); however, we question the age of this record. Similarly, *D. torquatus* is the only species of the genus occuring in Riss and Würm contexts in eastern Siberia (Vangengeim, 1961). These facts suggest that sediments of the Deering Formation which contain *D. henseli* fossils predate the replacement of that species by *D. torquatus;* that is, that they are at least of pre-Wisconsin age. Presence of *D. torquatus* in sediments immediately overlying the *D. henseli* zone also show that Unit 1 of the Deering Formation is no older than the Illinoian. In our opinion the sediments containing *D. henseli* fossils were probably deposited during early Illinoian time. Peat 4, immediately below the *D. henseli* zone at Station 8 must then represent a pre-Illinoian (Kotzebuian?) interglacial instead of the Sangamon intergalacial as suggested by McCulloch (1967). Peat 5, marking a prominent lithological change and representing temporary cessation of loess deposition probably represents the Sangamon interglacial.

PALEOECOLOGY

Stratigraphic evidence and alternate fossil evidence makes it possible to suggest the paleoautecology of the fossil mammals occurring at the Cape Deceit locality. Fossil insects from the *D. henseli* zone of the Deering Formation (Matthews, M.S. in preparation) indicate that the species occupied a tundra environment like the extant species *D. hudsonicus.* Evidence of solifluction and permafrost in the fossiliferous silts and sands of the Cape Deceit Formation shows that the mammals of the Cape Deceit Local Fauna also lived in a treeless (tundra?) environment. Thus, the evolution and early history of both *Microtus* and *Dicrostonyx* are associated with arctic environments.

The abundance of fossils in the Cape Deceit Local Fauna allows an assessment of mammalian paleosynecology (i.e., community structure). Table 2 is a comparison of the Cape Deceit Local Fauna with an aggregate fauna, excluding carnivores, from various contemporary tundra communities.

Two of the Cape Deceit taxa, *Equus* sp. and *Cervus* cf. *elaphus,* do not occur in contemporary Alaskan tundra environments. Both are grazers and both occupied late Pleistocene treeless communities in unglaciated Alaska (Guthrie, 1967, 1968b). Their presence in the Cape Deceit Local Fauna may indicate that early Pleistocene tundra environments of Alaska were as grassy as

TABLE 1

GEOLOGIC HISTORY OF THE CAPE DECEIT LOCALITY

Stratigraphic Unit	Events and probable paleoenvironments	Correlation	
		European	North American
Deering Formation			
Peat 6	Reduced silt deposition and moss-peat formation—Tundra	Holocene	Holocene
	Deposition of clayey silts in small ponds (Station 8)—Tundra	Würm (Weichsel)	Wisconsin
	Slight erosional interval		
Unit 2	Solifluction episode—active layer probably thicker than at present—Tundra: local climate slightly warmer than at present		
	Deposition of organic silts (rebedded loess)—Tundra		
Peat 5	Formation of nonwoody peat—Tundra	Eem	Sangamon (Interglacial)
	Loess deposition—little rebedding, short period of frost crack formation—Tundra	Riss (Saal)	Illinoian (= Nome River Glaciation, Seward Peninsula)
	Local erosion		
Unit 1	Deposition of organic silts (rebedded loess) and sands. *D. henseli* zone—Tundra		
	Formation of woody peat—Forested, climate warmer than at present and spruce treeline advanced at least to position of Cape Deceit (see Fig. 11)	Mindel/Riss? (Holstein)	Kotzebuan Transgression? (= Yarmouth?) (Interglacial)
Hiatus	Period of erosion and thaw. May coincide with peat formation (Peat 4) at Stations 8 and 9	Mindel/Riss?	Kotzebuan? (Interglacial)
Imnachuk Formation			
	Solifluction episode—active layer about as thick as at present—Tundra: local climate no more severe than at present		
Peat 3	Deposition of peatly silts. May coincide in part with following solifluction episode—Tundra?	Mindel? (Elster)	?
	Deposition of organic silts (rebedded loess) and sands—Tundra?		
Hiatus	Period of thaw followed by erosion Climate warmer than at present	Cromerian?	Einahnuhtan or Anvilian Transgression? (Interglacial)

TABLE 1 (continued)

GEOLOGIC HISTORY OF THE CAPE DECEIT LOCALITY

Stratigraphic Unit	Events and probable paleoenvironments	Correlation	
		European	North American
Cape Deceit Formation			
Peat 2	Formation of nonwoody peat—Tundra	Gunz II?	Iron Creek Glaciation?
	Deposition of organic silts (rebedded loess); evidence of periglacial features	(Menapian)	(Seward Peninsula)
Unit 2	Tundra: probably a more severe tundra environment than at present		
Peat 1	Formation of thick peat—Forest tundra—conifer treeline advanced to position of Cape Deceit. Local patches of tundra persist	Gunz I/Gunz II? (Waal)	? (Interglacial)?
Unit 1	Deposition of silts sands and gravels, primarily by solifluction. Some rapid deposition (flows?) of sandy silt—Tundra	Gunz I? (Eburonian?)	?
	Short? Non-depositional interval		
Kittik	Mechanical weathering of metalimestone bedrock and rebedding of weathering product—Cold climate		

the late Pleistocene tundra apparently was (Guthrie, 1968b). On the other hand, the few *Equus* and *Cervus* fossils from the Cape Deceit Formation do not allow an estimate of their quantitative importance in the ungulate community as has been done for late Pleistocene assemblages from Fairbanks (Guthrie, 1968b); therefore, they may not have been common in early Pleistocene tundra environments. And if this is so, then it might be argued, as Martin (1967) has done for other areas of North America, that both *Equus* and *Cervus* could exist as minor elements of contemporary tundra faunas, but don't because of the drastic effect of late Pleistocene human hunting.

The environment in which the Cape Deceit Local Fauna nammals lived was obviously a lowland tundra of some sort; yet two of the genera in that assemblage, *Marmota* and *Ochotona,* are presently restricted to more alpine areas in Alaska. But marmots and ochotonids do occur in lowland tundra and steppe areas of Eurasia (Ognev, 1947). For example, *Ochotona pusilla,* the steppe pika of southern Russia, and *O. daurica,* from southern Siberia, both occur in lowland treeless environments where they inhabit thickets or other sheltered areas such as ravines or river banks (Ognev, 1940). Thus, not all pikas occupy scree slopes like the two North American species; indeed, the large size of *O. whartoni* seems to preclude its having lived in such areas. Its habitat requirements were probably more similar to those of the Eurasian steppe pikas.

Table 2 illustrates some possible examples of ecologic replacement. For example, *Clethrionomys rutilus,* a seed eater with rooted check teeth somewhat similar to those of *Pliomys,* may occupy the niche formerly occupied by *Pliomys decringensis. Dicrostonyx torquatus,* a contemporary resident of lowland tundra on the Seward Peninsula, no doubt occupies the niche formerly filled by *Predictostonyx hopkinsi;* although, if *Ochotona whartoni* fed on grasses like some extant ochotonids, it might have shared this niche with *P. hopkinsi.*

Table 3 shows the combined relative and

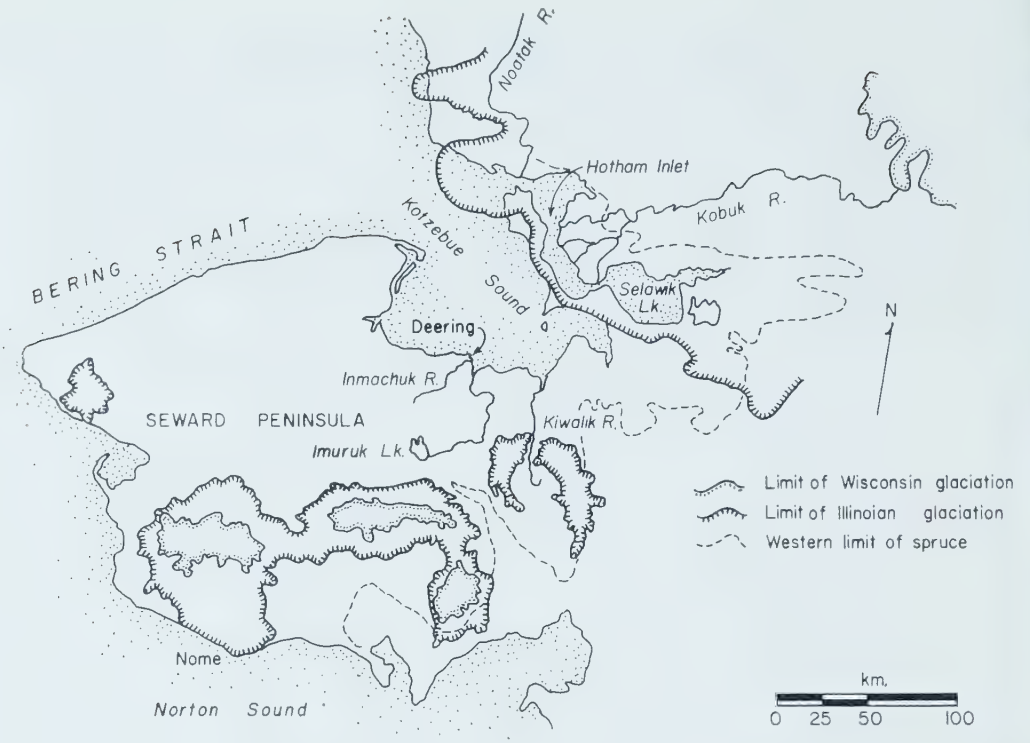


FIG. 11. Seward Peninsula region: showing distribution of late Pleistocene glaciers, present western limit of spruce forest, and localities mentioned in text.

absolute abundance of the four most important small mammal taxa in the Cape Deceit Local Fauna. The relative abundance of these taxa in each of the separate sieved samples was similar to that in the combined presentation of Table 3. Fossils of *Lemmus* are an important part of the assemblage even though they and fossils of *Pliomys* are less abundant than those of *Predicrostonyx* and *Microtus*. Without knowing the specific microhabitat requirements of the extinct species in Table 3, it is difficult to interpret differences in relative abundance. Note, however, that *Plimoys deeringensis*, whose teeth suggest seed-eating habits, represents 20% of the assemblage in Table 3. Fossil seeds are extremely abundant in the bedded, fossiliferous silts of Unit 2 (Cape Deceit Formation). Also, as we mentioned earlier, individuals of *Lemmus* cf. *sibericus* from the Cape Deceit Local Fauna may have occupied moist areas in regions of Ice-wedge polygons like the living members of *L. sibericus*. Recall the evidence for ice wedges in Unit 2 of the Cape Deceit Formation. Solifluction folds in Unit 1 also imply moist soil conditions.

EVOLUTIONARY RATES

Most discussions of microtine evolution stress the rapid and almost unidirectional increase in tooth complexity. The Cape Deceit Local Fauna illustrates both of these trends in *Microtus, Pliomys,* and the *Predicrostonyx–Dicrostonyx* lineage. On the other hand, species of *Lemmus* have remained virtually unchanged (at least in dentition) in much the same way as have species of the two sciurid genera *Marmota* and *Citellus*.

The most spectacular evolutionary change occurred in the *Predicrostonyx–Dicrostonyx* lineage. It is one of the more rapid direc-

TABLE 2

COMPARISON OF AN AGGREGATE OF CONTEMPORARY TUNDRA COMMUNITIES WITH THE CAPE DECEIT LOCAL FAUNA [a]

Cape Deceit local fauna	Contemporary tundra
Marmota sp.	*Marmota caligata*
Citellus sp.	*Citellus parryi*
Predicrostonyx hopkinsi	*Dicrostonyx torquatus*
Lemmus cf. *sibericus*	*Lemmus sibericus*
Microtus deceitensis	*Microtus oeconomus*
	M. miurus
Pliomys deeringensis	*Clethrionomys rutilus*
Ochotona whartoni	*Ochotona collaris*
	Lepus timidus
Sorex (*Sorex*) sp.	*Sorex arcticus*
Rangifer sp.	*Rangifer tarandus*
	Alces alces
	Ovis nivicola
Cervus cf. *elaphus*	
Equus sp.	

[a] Carnivores excluded

tional changes documented in mammalian evolution, and, unlike some other examples of rapid evolution (i.e., *Equus*), apparently occurred with a minimum of phylogenetic branching. Another genus (not represented in the Cape Deceit assemblage) which evolved as rapidly is *Mammuthus (=Elaphus)*. As in the *Predicrostonyx–Dicrostonyx* lineage, the most striking evolutionary change among the elephants was in the enamel complexity of the dental battery. The extant *D. torquatus* and the extinct *Mammuthus primigenius* are the microtine and proboscidian species with the most complex dentition. To attain this level of complexity both genera have added lophs or triangles, narrowed the lophs or triangles anteroposteriorly, and acquired enamel specializations. The rapid and analogous evolution of *Mammuthus and Dicrotonyx* occurred at about the same time–mid-Pleistocene—and in the same region—Holarctica. Only the size difference of the two genera obscures the similarity of the niche they occupy—one is a macrograzer; the other a micrograzer. The selection pressure responsible for these evolutionary changes may have been the development and expansion of tundra-steppe environments. Such environments might have also offered

TABLE 3

ABSOLUTE AND RELATIVE ABUNDANCE OF INDIVIDUAL TEETH FROM SMALL MAMMALS OF THE CAPE DECEIT LOCAL FAUNA

	Predicrostonyx	Microtus	Pliomys	Lemmus	Total
M^1	23 (31.5%)	25 (34.2%)	14 (19.3%)	11 (15%)	73
M^2	18 (32.7%)	19 (34.5%)	11 (20%)	7 (12.7%)	55
M^3	11 (26.2%)	18 (42.8%)	5 (11.9%)	8 (19%)	42
M_1	30 (34.1%)	29 (32.9%)	12 (13.6%)	17 (19.3%)	88
M_2	26 (33.7%)	28 (36.3%)	7 (9.1%)	16 (20.8%)	77
M_3	21 (33.3%)	9 (14.2%)	7 (11.1%)	16 (25.4%)	63

a new evolutionary potential for genera such as *Bison* and the small mammal *Allophaiomys,* both of which occurred in southern Asia during the early Pleistocene (Kurten, 1968; Adamenko and Zazhigin, 1965).

The very slow rate of *Lemmus* evolution contrasts with the rapid rates mentioned above. Failure of *Lemmus* to evolve significantly while other microtines were undergoing marked evolutionary changes probably means that the specialized habitat which *Lemmus* occupies was constantly available even while the regional character of treeless northern environments was changing.

A stylized illustration of the differing evolutionary rates in the *Predicrostonyx–Dicrostonyx, Microtus,* and *Lemmus* lineages is presented in Fig. 12. The straight lines are surely abstractions of what were probably irregular evolutionary rates. In the diagram of *Microtus, M. deceitensis* is contrasted with the complex-toothed *M. pennsylvanicus* rather than the more common Alaskan species, *M. oeconomus.* Note in Fig. 12 how individual teeth within the same lineage have different evolutionary rates.

ZOOGEOGRAPHY

It has been traditional for paleozoogeographers to consider the Beringian area as a filter corridor of Palaearctic–Nearctic faunal exchange. While this is probably an acceptable practice when dealing with Tertiary mammals, we feel that it tends to misrepresent the zoogeographical relationships of Pleistocene mammals. The European and North American record of fossil mammals, especially when considered in the light of the Cape Deceit Local Fauna, supports this statement.

European Pleistocene mammal literature is replete with references to the sudden appearance of tundra or steppe-adapted allochthonous mammals. Chaline and Michaux (1969) and Kowalski (1966) allude to this characteristic of the small mammal record. Durtén (1968) provides large mammal examples—*Rangifer, Ovibos, Cervus elaphus,* and *Bison.* These taxa and the small mammals *Microtus* and *Dicrostonyx* also appear with equal abruptness, lacking antecedents, in the central Nearctic (Hibbard *et al.,* 1965); therefore, their center of evolution must have been eastern Eurasia and Alaska. A similar proposal has been made by Hoffmann and Taber (1967), but they considered the evolutionary center to be restricted to the Palaearctic. Our data show that Alsaka must be included.

It should not be assumed, however, that

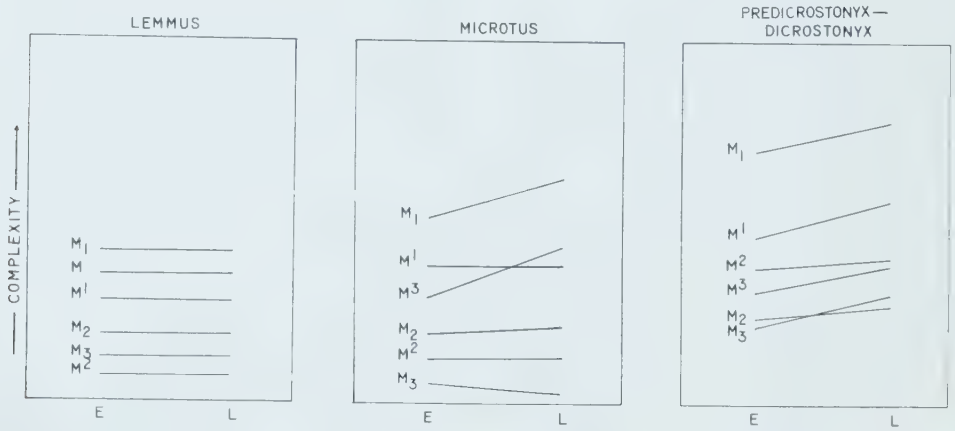


FIG. 12. Dental complexity changes occurring during Pleistocene in three microtine lineages represented in the Cape Deceit Local Fauna. E=early Pleistocene; L=late Pleistocene.

because the earliest record of genera such as *Rangifer* and *Microtus* occurs in the Nearctic, it is necessarily the area in which they originated. If, as Chaline (1966) believes, *Microtus* is derived from the Palaearctic microtine *Allophaiomys pliocaenicus,* then that step probably took place in eastern Asia since the easternmost record of *Allophaiomys* is from the western Altai (Admenko and Zazhigin, 1965). Actually the exact continent of origin is rather unimportant, for Alaska and Asia were joined across the Bering Land Bridge for much of the Pleistocene (Hopkins, 1967a).

The North American record of the influx of Eurasian–Alaskan arctic mammals differs in one important respect from the analogous event in the western Palaearctic. In North America it did not occur until the late Pleistocene (except for *Microtus*) (Hibbard *et al.,* 1965); whereas in Eruope it was a mid-Pleistocene phenomenon (Kurten, 1968). Prior to the discovery of the Cape Deceit site, this distinction was taken to include Alaska as well, and it led to the suggestion that Beringia had acted as a Pleistocene filter bridge for Palaearctic mammals. Now, of course, an alternative explanation must be found.

We believe the difference in timing of the appearance of arctic mammals in Europe and North America is the result of the physiographic and geographic differences of those two areas. For example, the northern position of Europe and the east–west orientation of its dominant mountain system, the Alps, resulted in its being connected with Asia and even Alaska by a wide periglacial tundra corridor during the Pleistocene. West (1969) has shown that a periglacial environment existed in East Anglia (Great Britain) during the latter part of the early Pleistocene (Beestonian). This is one of the earliest records of a severe arctic climate in western Europe and it coincides approximately with the first appearance in Europe of arctic-adapted mammals. In North America the situation is markedly different. Continental glaciers there extended farther south than in Europe, and, judging from the late Pleistocene condition, there was only a narrow zone of tundra near the ice margin. Providing Guilday (1963) is correct in his assumption that *Dicrostonyx hudsonius* is a relict—competitively inferior to *D. torquatus*—then the occurrence of both species in the ice-marginal tundra zone (*D. hudsonius,* Pennsylvania; *D. torquatus,* Idaho) Guilday *et al.,* 1964; Guilday, 1968) shows that the zone was not continuous. Synchronous glaciation of the north–south trending Cordilleran mountain system and central Canada also had the effect of disrupting the continuity of the Nearctic portion of the tundra biome. Alaskan tundra was either partially or completely isolated from the remainder of the Nearctic. Taylor (1965) also shows that cold climates did not exist in the unglaciated portions of west central North America (except at the ice margin) until late Pleistocene time. It is, therefore, no coincidence that mammals of arctic affinities do not appear there until the late Pleistocene.

Contemporary tundra mammalian faunas are not simply a mix of facultative tundra inhabitants derived from more southern areas of the Palaearctic and Nearctic. Instead, they consist primarily of obligate tundra inhabitants (*Dicrostonyx, Lemmus,* etc.) or other mammals such as *Rangifer* and *Citellus undulatus* whose primary habitat is tundra but which nevertheless occur also in boreal communities. The Cape Deceit Local Fauna shows that this distinctive aspect of tundra faunas has a lengthy historical basis; that is, even by mid-Pleistocene time tundra faunas such as the one which occupied the periglacial environment at Cape Deceit are more similar to contemporary and late Pleistocene tundra faunas than to contemporary boreal faunas. This is true of individual taxa as well. *Predicrostonyx hopkinsi,* which we know was a tundra in-

habitant, clearly foreshadows subsequent morphological features of the obligate tundra inhabiting microtines, *Dicrostonyx torquatus* and *D. hudsonius*. *Lemmus* had also apparently achieved its particular tundra adaptations by the mid-Pleistocene.

The Cape Deceit Local Fauna could be said to have "Palaearctic affinities," but we reject this epithet and its implications because it obscures evidence for the long-term evolutionary unity of tundra faunas. Instead, we prefer to think of it as representing a Beringian mammalian fauna which has been evolving independently of more southern Palaearctic and Nearctic mammalian faunas since at least latest early Pleistocene time.

The limits of this faunal realm correspond with the limits of lowland tundra, extensive tracts of which probably did not exist in the northern hemisphere until the late Pliocene or early Pleistocene (Hopkins *et al.*, 1971). The first mammals to occupy lowland tundra sites were probably derived directly from neighboring boreal communities. By the mid-Pleistocene, however, *in situ* evolution within the Beringian realm had produced initial members of the tundra-adapted *Microtus, Lemmus, Dicrostonyx,* and *Rangifer* lineages. Other lineages, represented by *Mammuthus, Bison, Equus,* and *Marmota,* originated elsewhere in the Palaearctic and Nearctic, but entered northern tundra regions by mid-Pleistocene time and subsequently became important members of the Beringian mammalian realm. Some of these lineages, i.e., *Dicrostonyx, Mammuthus,* show striking specializations such as the evolution of complex dentition suitable for processing siliceous plant material. This trend, culminating in the late Pleistocene, suggests what paleobotanical evidence has shown less equivocally—that late Pleistocene arctic treeless environments were more steppe-like than their earlier counterparts (Frenzel, 1968; Giterman and Golubeva, 1967). This character of late Pleistocene tundra is revealed by other features of the Beringian mammal fauna. For example, the central Asian steppe microtine *Lagurus lagurus* was sympatric with *Dicrostonyx torquatus* in late Pleistocene England (Kowalski, 1967). Another present-day Eurasian steppe inhabitant, *Saiga,* occurred in late Pleistocene western Europe and Alaska. The steppe influence in the latter area is also revealed by late Pleistocene mammalian assemblages which are dominated by fossils of grazing ungulates—*Bison, Mammuthus,* and *Equus* (Guthrie, 1968b).

Finally, although intercontinental migration is deemphasized in our concept of an independent Beringian mammalian realm, some mammals clearly did move from the Palaearctic to the Nearctic quite rapidly, probably because they had no competitors in the Beringian realm. One of the best examples is the genus *Homo*.

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